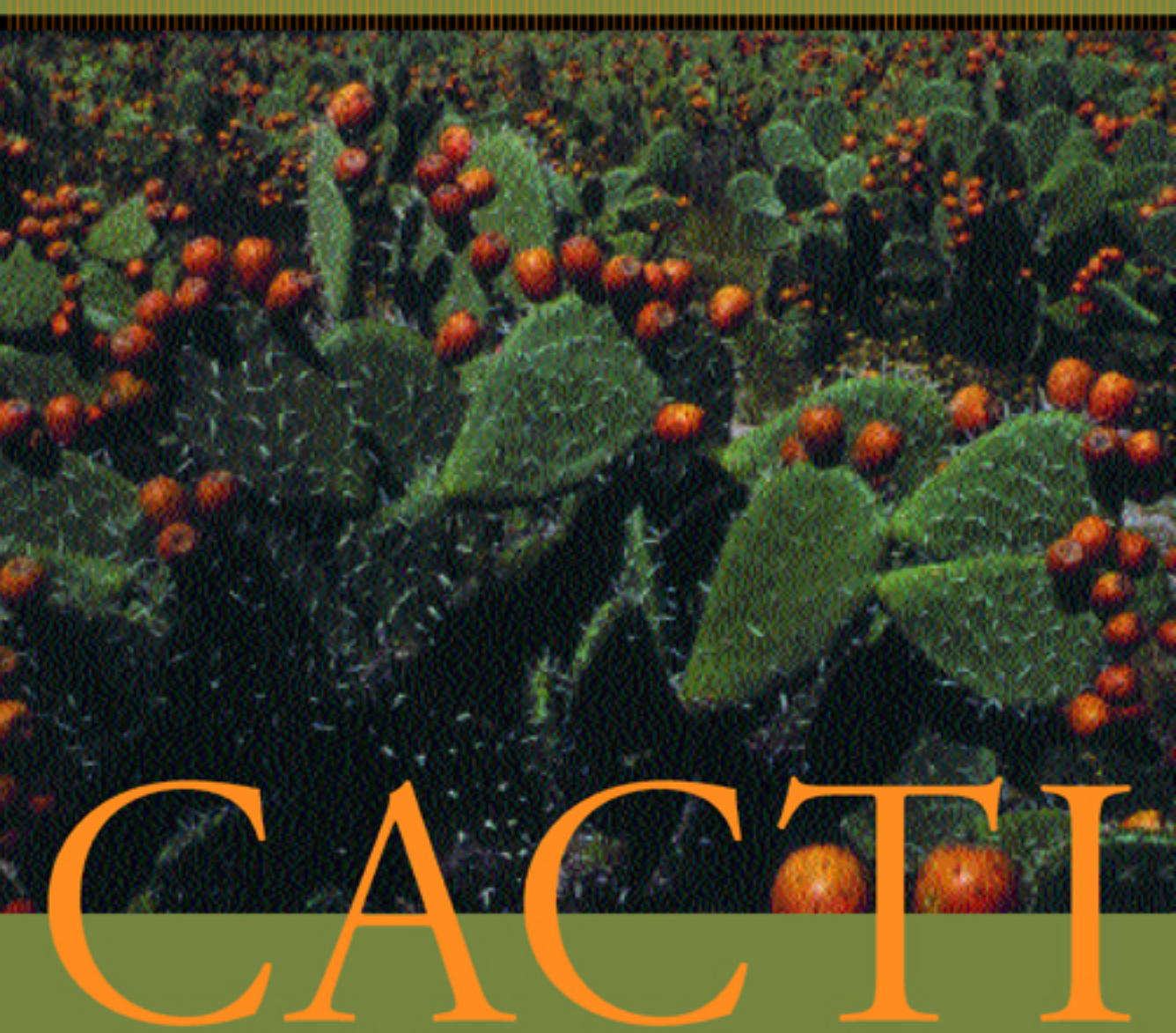


CACTI

EDITED BY PARK S. NOBEL

BIOLOGY AND USES

VISIT…



CACTI

CACTI

BIOLOGY AND USES

Edited by Park S. Nobel

UNIVERSITY OF CALIFORNIA PRESS
Berkeley Los Angeles London

University of California Press
Berkeley and Los Angeles, California

University of California Press, Ltd.
London, England

© 2002 by the Regents of the University of California

Library of Congress Cataloging-in-Publication Data

Cacti: biology and uses / Park S. Nobel, editor.
p. cm.
Includes bibliographical references (p.).
ISBN 0-520-23157-0 (cloth : alk. paper)
1. Cactus. 2. Cactus—Utilization. I. Nobel, Park S.

QK495.C11 C185 2002
583'.56—dc21 2001005014

Manufactured in the United States of America
10 09 08 07 06 05 04 03 02 01
10 9 8 7 6 5 4 3 2 1

The paper used in this publication meets the minimum requirements of
ANSI/NISO Z39.48–1992 (R 1997) (*Permanence of Paper*).

CONTENTS

List of Contributors · vii
Preface · ix

1. Evolution and Systematics
Robert S. Wallace and Arthur C. Gibson · 1

2. Shoot Anatomy and Morphology
Teresa Terrazas Salgado and James D. Mauseth · 23

3. Root Structure and Function
Joseph G. Dubrovsky and Gretchen B. North · 41

4. Environmental Biology
Park S. Nobel and Edward G. Bobich · 57

5. Reproductive Biology
Eulogio Pimienta-Barrios and Rafael F. del Castillo · 75

6. Population and Community Ecology
Alfonso Valiente-Banuet and Héctor Godínez-Alvarez · 91

7. Consumption of Platyopuntias by Wild Vertebrates
Eric Mellink and Mónica E. Riojas-López · 109

8. Biodiversity and Conservation
Thomas H. Boyle and Edward F. Anderson · 125

9. Mesoamerican Domestication and Diffusion
Alejandro Casas and Giuseppe Barbera · 143

10. Cactus Pear Fruit Production
Paolo Inglese, Filadelfio Basile, and Mario Schirra · 163

11. Fruits of Vine and Columnar Cacti
Avinoam Nerd, Noemi Tel-Zur, and Yosef Mizrahi · 185

12. Forage, Fodder, and Animal Nutrition
Ali Nefzaoui and Hichem Ben Salem · 199

13. Nopalitos, Mucilage, Fiber, and Cochineal
Carmen Sáenz-Hernández, Joel Corrales-Garcia, and Gildardo Aquino-Pérez · 211

14. Insect Pests and Diseases
Helmuth G. Zimmermann and Giovanni Granata · 235

15. Breeding and Biotechnology
Brad Chapman, Candelario Mondragon Jacobo, Ronald A. Bunch, and Andrew H. Paterson · 255

Index · 273

CONTRIBUTORS

Edward F. Anderson (Deceased), Desert Botanical Garden, Phoenix, Arizona

Gildardo Aquino-Pérez, Insituto de Recursos Genéticos y Productividad, Montecillo, Mexico

Giuseppe Barbera, Istituto di Coltivazioni Arboree, Università degli Studi di Palermo, Italy

Filadelfio Basile, Dipartimento Scienze Economico-Agrarie ed Estimativ, Universita degli Studi di Catania, Italy

Hichem Ben Salem, Institut National de la Recherche Agronomique de Tunisie, Laboratoire de Nutrition Animale, Ariana, Tunisia

Edward G. Bobich, Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles

Thomas H. Boyle, Department of Plant and Soil Sciences, University of Massachusetts, Amherst

Ronald A. Bunch, D'Arrigo Bros. Co., Salinas, California

Alejandro Casas, Departamento de Ecología de los Recursos Naturales, Instituto de Ecología, Universidad Nacional Autónoma de México, Morelia

Brad Chapman, Plant Genome Mapping Laboratory, University of Georgia, Athens

Joel Corrales-García, Departamento de Ingeniería Agroindustrial, Universidad Autónoma de Chapingo, Mexico

Rafael F. del Castillo, Centro Interdisciplinario de Investigacíon para el Desarrollo Integral Regional Unidad Oaxaca, Mexico

Joseph G. Dubrovsky, Departamento de Biología Molecular de Plantas, Instituto de Biotecnología, Universidad Nacional Autónoma de México, Cuernavaca

Arthur C. Gibson, Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles

Héctor Godínez-Alvarez, Departamento de Ecología Funcional y Aplicada, Instituto de Ecología, Universidad Nacional Autónoma de México, Mexico City

Giovanni Granata, Dipartimento di Scienze e Technologie Fitosanitartie, Università degli Studi di Catania, Italy

Paolo Inglese, Istituto di Coltivazioni Arboree, Palermo, Italy

James D. Mauseth, Department of Integrative Biology, University of Texas at Austin

Eric Mellink, Centro de Investigación Cientifica y de Educación Superior de Ensenada, Mexico

Yosef Mizrahi, Department of Life Sciences and Institutes for Applied Research, Ben-Gurion University of the Negev, Israel

Candelario Mondragon Jacobo, Programa de Nopal y Frutales, Instituto Nacional de Investigaciones Forestales y Agropecuarias, Queretaro, Mexico

Ali Nefzaoui, Institut National de la Recherche Agronomique de Tunisie, Laboratoire de Nutrition Animale, Ariana, Tunisia

Avinoam Nerd, Institutes for Applied Research, Ben-Gurion University of the Negev, Israel

Park S. Nobel, Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles

Gretchen B. North, Department of Biology, Occidental College, Los Angeles, California

Andrew H. Paterson, Plant Genome Mapping Laboratory, University of Georgia, Athens

Eulogio Pimienta-Barrios, Departamento de Ecología, Centro Universitario de Ciencias Biológicas y Ambientales, Universidad de Guadalajara, Mexico

Mónica E. Riojas-López, Departamento de Ecología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Mexico

Carmen Sáenz-Hernández, Departamento de Agroindustria y Enología, Facultad de Ciencias Agrarias y Forestales, Universidad de Chile, Santiago

Mario Schirra, Instituto per la Fisologia della Maturazione e della Conservazione del Frutto delle Specie Arboree Mediterranee, Oristano, Italy

Noemi Tel-Zur, Department of Life Sciences, Ben-Gurion University of the Negev, Israel

Teresa Terrazas Salgado, Programa de Botánica, Colegio de Postgraduados, Montecillo, Mexico

Alfonso Valiente-Banuet, Departamento de Ecología Funcional y Aplicada, Instituto de Ecología, Universidad Nacional Autónoma de México, Mexico City

Robert S. Wallace, Department of Botany, Iowa State University, Ames

Helmuth G. Zimmermann, Plant Protection Research Institute, Agricultural Research Council, Pretoria, South Africa

PREFACE

The Cactaceae, a family of approximately 1,600 species, is native to the New World but is cultivated worldwide. In response to extreme habitats, cacti have evolved special physiological traits as well as distinctive appearances. The stem morphology, spine properties, and often spectacular flowers have caused hobbyists to collect and cultivate large numbers of cacti. Both cactus form and function relate to nocturnal stomatal opening and Crassulacean acid metabolism, which lead to efficient use of limited soil water. Thus, cacti can thrive in arid and semiarid environments, where they are often important resources for both wildlife and humans. Indeed, cacti have been consumed by humans for more than 9,000 years. Currently, *Opuntia ficus-indica* is cultivated in over 20 countries for its fruit, and an even greater land area is devoted to its cultivation for forage and fodder. The fruits of other cactus species, known as pitahayas and pitayas, and various other cactus products are appearing in an increasing number of markets worldwide.

Due to the high water-use efficiency and other adaptations of cacti, biological and agronomic interest in them has soared. From 1998 to 2000, more than 600 researchers published over 1,100 articles on cacti, including papers in proceedings of national and international meetings. Yet a current, synthetic, widely ranging reference is not available. This book, which consists of a series of authoritative, up-to-date, review chapters written by established experts as well as new contributors, emphasizes both the biology of cacti and their uses. Twelve authors are from Mexico, eleven from the United States, five from Italy, three from Israel, two from Tunisia, and one each from Chile and South Africa. Most of the authors share my interests in basic research on the Cactaceae. Nearly half of the authors, especially those dealing with agronomic aspects, are involved with the CactusNet sponsored by the Food and Agricultural Organization of the United Nations. Approximately 1,300 references are cited in the chapters, which not only indicate the widespread interest in cacti but also should facilitate further investigations. The intended audience ranges from ecologists and environmentalists to agriculturalists and consumers to cactus hobbyists and enthusiasts.

The point of departure is the evolution of the family in the broad sense, paying particular attention to new molecular and genetic approaches (Chapter 1). People recognize cacti by their shoot morphology, which reflects various cellular characteristics (Chapter 2). The uptake of water and nutrients from the soil by roots that sustains the shoots has unique features as well (Chapter 3). Survival depends on adaptation to abiotic environmental conditions, which cacti have done in special ways (Chapter 4). In addition to enduring harsh conditions, cacti must reproduce, for which many strategies have evolved (Chapter 5). Biotic factors are also crucial for the success of cacti in natural environments (Chapter 6). Because of their ecological success, cacti are important food resources for wild vertebrates

(Chapter 7). The many unique characteristics of the Cactaceae have attracted collectors and raised concerns about issues of biodiversity and conservation (Chapter 8) as well as led to their ancient usage and subsequent wide diffusion by humans (Chapter 9). The most widespread use occurs for fruits of platyopuntias, known as cactus pears (Chapter 10). Also, fruits of vine-like and columnar cacti are increasingly popular in many countries (Chapter 11). An even greater land area worldwide than is used for cactus fruits is devoted to raising platyopuntias for forage and fodder (Chapter 12). Besides such uses, cacti are also important as a vegetable, as a dietary supplement, and as the host for the red-dye-producing cochineal (Chapter 13). Such uses, which are constrained by pests and diseases (Chapter 14), are currently expanding via breeding and biotechnology (Chapter 15).

Special thanks are due to those who helped in the realization of this book. Edward Bobich helped prepare the line drawings and halftones for reproduction, and Erick De la Barrera assisted with the many Spanish citations. Marian McKenna Olivas competently did line editing, and Alicia Materi meticulously typed the developmental and line editing changes. Financial support for these steps was provided by Sol Leshin, a man of integrity and generosity with a profound interest in plants and their uses dating back to his M.S. in soil science in 1938. Numerous suggestions on improving the arrangement and scientific content were the result of a graduate course taught from the book and attended by Edward Bobich, Erick De la Barrera, C. J. Fotheringham, Catherine Kleier, and Alexandra Reich. The dedication and important suggestions of these people helped meld the contributions of a diverse group of authors into the final product, for which I am extremely grateful.

Park S. Nobel
February 10, 2001

CHAPTER

› 1 ‹

EVOLUTION AND SYSTEMATICS

Robert S. Wallace and Arthur C. Gibson

Introduction
Phylogenetic Placement of Cactaceae
Cactaceae, a Family of Order Caryophyllales
Classification of Cactaceae within Suborder Portulacineae
Cactaceae, a Monophyletic Family
Defining Subfamilies of Cactaceae
Transitions from Structural Analyses to Molecular Systematics
Molecular Systematics of Cactoideae
Identifying the Oldest Taxa
Epiphytic Cacti
Columnar Cactus Lineages
Cacteae and Notocacteae
Solving Classification Problems Using Molecular Techniques
Phylogenetic Studies of Subfamily Opuntioideae
New Insights into Cactus Evolution
Structural Properties
Revised Biogeographic Models Based on Molecular Studies
Concluding Remarks
Literature Cited

Introduction

The Cactaceae is one of the most popular, easily recognizable, and morphologically distinct families of plants, and it includes approximately 1,600 species (Gibson and Nobel 1986; Barthlott and Hunt 1993). Cacti occur in the New World from western and southern Canada (Speirs 1982) to southern Patagonia in Chile and Argentina (Kiesling 1988), and the epiphytic genus *Rhipsalis* has dispersed naturally, undoubtedly by birds, to tropical Africa and Madagascar and across to Sri Lanka and southern India (Thorne 1973; Barthlott 1983). These usually spiny organisms (Fig. 1.1) are loved by plant fanciers for their diverse forms and showy flowers. Nearly every introductory college biology or ecology textbook contains at least one cactus photograph, used to illustrate plant adaptation to dry habitats. Important commercial products are derived from cacti (Nobel 1994, 1998). Cacti have also helped evolutionary biologists and ecologists understand CAM (Crassulacean acid metabolism) and succulence (Gibson and Nobel 1986; Nobel 1988, 1991).

In some plant families, it is merely a matter of con-

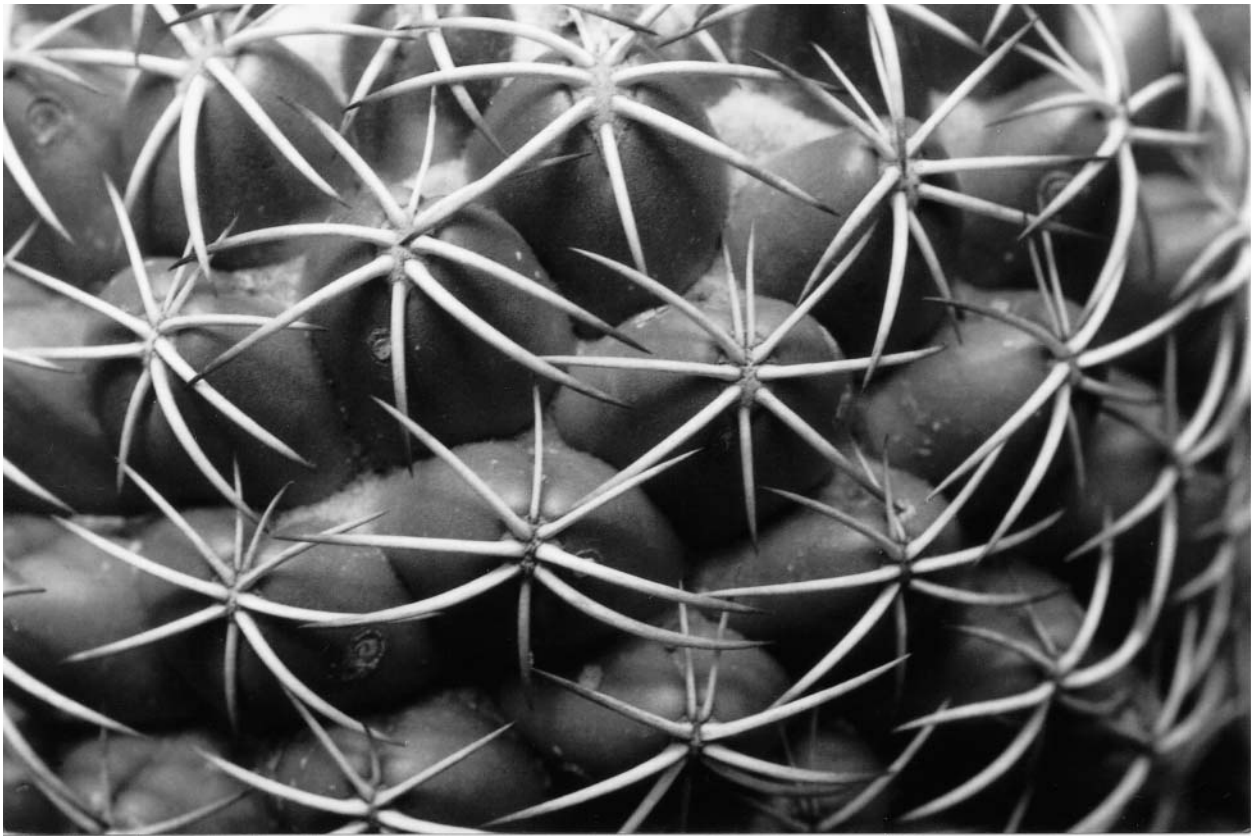


Figure 1.1. The vegetative plant of *Coryphantha bumamma* (Ehrenberg) Brittton and Rose (tribe Cacteae), a low-growing spherical cactus from Guerrero, Mexico.

venience to have correct names for plant species. In the Cactaceae, however, there is not only a huge demand for correct names and precise classification into genera, but also a critical need for a phylogenetic classification because there are many subjects, some of which are covered in this book, that depend on having an accurate evolutionary reconstruction of cactus history.

Phylogenetic Placement of Cactaceae

Cactaceae, a Family of Order Caryophyllales

Family Cactaceae is assigned to order Caryophyllales, which includes, among others, ice plants (Aizoaceae), portulacas (Portulacaceae), carnations (Caryophyllaceae), bougainvilleas (Nyctaginaceae), pokeweeds (Phytolaccaceae), amaranths (Amaranthaceae), and saltbushes (Chenopodiaceae). The taxonomic history of classifying Cactaceae within this order has been adequately reviewed (Cronquist and Thorne 1994), and there is universal acceptance that cacti are core members of Caryophyllales.

Phylogenetic placement within the Caryophyllales is undisputed, because cacti and other families within the order share derived characters, i.e., synapomorphies, that do not occur in any other angiospermous order. One structural synapomorphy, and the first recognized feature for relating these families, is that the seed contains a strongly curved, peripheral embryo around a central nutritive perisperm, not endosperm. From that observation arose the ordinal name Centrospermae (Eichler 1878). A chemical synapomorphy is the occurrence of betalains, a class of nitrogenous pigments derived from tyrosine (Mabry 1964; Clements et al. 1994). The Cactaceae and closely related families form a proteinaceous plastid inclusion (designated as type P3cf) during the ontogeny of sieve-tube members (Behnke 1976a,b, 1994). Congruence of the three mentioned unlinked and unique synapomorphic characters in these same families, not in others, formed a solid case for recognizing this monophyletic clade.

Order Caryophyllales, which was established by analyzing certain types of structural and chemical data, was tested with a new data set using chloroplast DNA (cpDNA) restriction site mutations, and was confirmed by the loss of the *rpl*2 intron in the common ancestor of the order (Downie and Palmer 1994). Indeed, investigators use

whatever data are available at the time to formulate an initial hypothesis, and later test the model using an indisputable data set of a totally different nature that provides resolution. Yet there are still some unresolved issues concerning the composition of Caryophyllales and whether other families, shown by molecular studies to share closest DNA affinities to Caryophyllales, should be classified within the order (Angiosperm Phylogeny Group 1998). Among these are the insectivorous sundews (Droseraceae) and pitcher plants of Nepenthaceae. It is unclear at this time whether molecular data will require these nontraditional members to be classified within the order or instead as allies in one or more separate orders. Regardless of that outcome, placement of family Cactaceae is unaffected for the time being.

Classification of Cactaceae within Suborder Portulacineae

Phylogenetic relationships of the Cactaceae within the Caryophyllales have been much more difficult to determine. Investigators have been interested in determining to which of the betalain-containing families Cactaceae is phylogenetically most closely related. Traditional comparative and developmental evidence favored the Aizoaceae (Turner 1973; Rodman et al. 1984) or Phytolaccaceae (Buxbaum 1953; Cronquist 1981), emphasizing floral features. More recent analyses claimed that the Cactaceae has most recent ancestry with the Portulacaceae (Thorne 1983; Gibson and Nobel 1986; Hershkovitz 1991; Gibson 1994), within what became called suborder Portulacineae Thorne (Cronquist and Thorne 1994), which included Cactaceae, Portulacaceae, Didiereaceae, and Basellaceae.

New data sets from gene sequence experiments tested the model and strongly supported Portulacineae as a monophyletic taxon that includes Cactaceae (Manhart and Rettig 1994). Cactaceae and certain Portulacaceae are sister taxa sharing a 500 base-pair (bp) deletion in the Rubisco gene *rbc*L (Rettig et al. 1992; Downie and Palmer 1994). Using a 1,100 bp sequence of open reading frame in cpDNA, the largest gene in the chloroplast genome, Downie et al. (1997) concluded again that *Pereskia* (Cactaceae) belongs in the portulacaceous cohort. With internal transcribed spacer sequences of cpDNA, Hershkovitz and Zimmer (1997) obtained results that placed the primitive leaf-bearing cacti phylogenetically nested within the Portulacaceae, and the Cactaceae was identified as the sister taxon of a clade that includes species of *Talinum.* In a more intensive cpDNA analysis of the portulacaceous cohort, using gene sequence data of *ndh*F, a recent study has shown that the Cactaceae is indeed nested within the Portulacaceae sensu lato and is most closely related to *Talinum* and *Portulaca* (Fig. 1.2; Appleqvist and Wallace 2001). In future systematic studies of the family, these sequence data will play an important role in redefining the family Portulacaceae, as well as the evolutionarily distinct groups it now contains, and how the evolutionary components of this diverse clade need to be circumscribed.

Cactaceae, a Monophyletic Family

Even casual students of cacti can recognize the repetitive vegetative design within this plant family (Gibson and Nobel 1986). Typically, a cactus possesses a perennial photosynthetic succulent stem, bearing leaf spines produced on modified axillary buds, termed areoles, but lacking broad green leaves. The colorful flower of the typical cactus has many separate perianth parts, numerous stamens, and an inferior ovary with many ovules and parietal placentation. The fruit is a many-seeded berry, often juicy but in some taxa becoming dry or splitting open at maturity. There are, of course, exceptional forms: (1) spineless plants (e.g., certain epiphytes such as *Disocactus* and *Epiphyllum* and small cacti such as *Lophophora* and *Ariocarpus*); (2) geophytes with annual above-ground shoots (e.g., *Pterocactus kuntzei, Opuntia chaffeyi,* and *Peniocereus striatus*); (3) primitive cacti that have relatively broad, dorsiventrally flattened leaves (e.g., *Pereskia* spp. and *Pereskiopsis porteri*); (4) plants that have relatively small flowers with fewer parts (e.g., small-flowered species of *Rhipsalis, Pseudorhipsalis,* and *Uebelmannia* spp.); and (5) superior ovaries with axile placentation (e.g., *Pereskia sacharosa*). None of these exceptions is troubling, because all are well-accepted members of the family and understood as representing either primitive or highly reduced, apomorphic (derived) states of cactus features.

The morphological distinctiveness and monophyly of family Cactaceae have been further supported conclusively with molecular data. There has occurred a 6 kb inversion in the large single copy region of the plastid genome (relative to the consensus land plant gene order seen in *Nicotiana tabacum;* Downie and Palmer 1993) that involves the genes *atp*E, *atp*B, and *rbc*L. This cpDNA inversion has been found in all cacti sampled, so this is an excellent molecular synapomorphy for defining Cactaceae (Wallace 1995; Wallace and Forquer 1995; Wallace and Cota 1996; Cota and Wallace 1996, 1997). Remarkably, an identical inversion of the same cpDNA region occurs independently in another caryophyllalean lineage, the Chenopodiaceae (Downie and Palmer 1993). Nonetheless, because cacti consistently exhibit this 6 kb inversion, molecular systematists infer that Cactaceae are monophyletic, i.e., traceable back to a single ancestral population in which the inversion appeared and then became genetically fixed. What remains

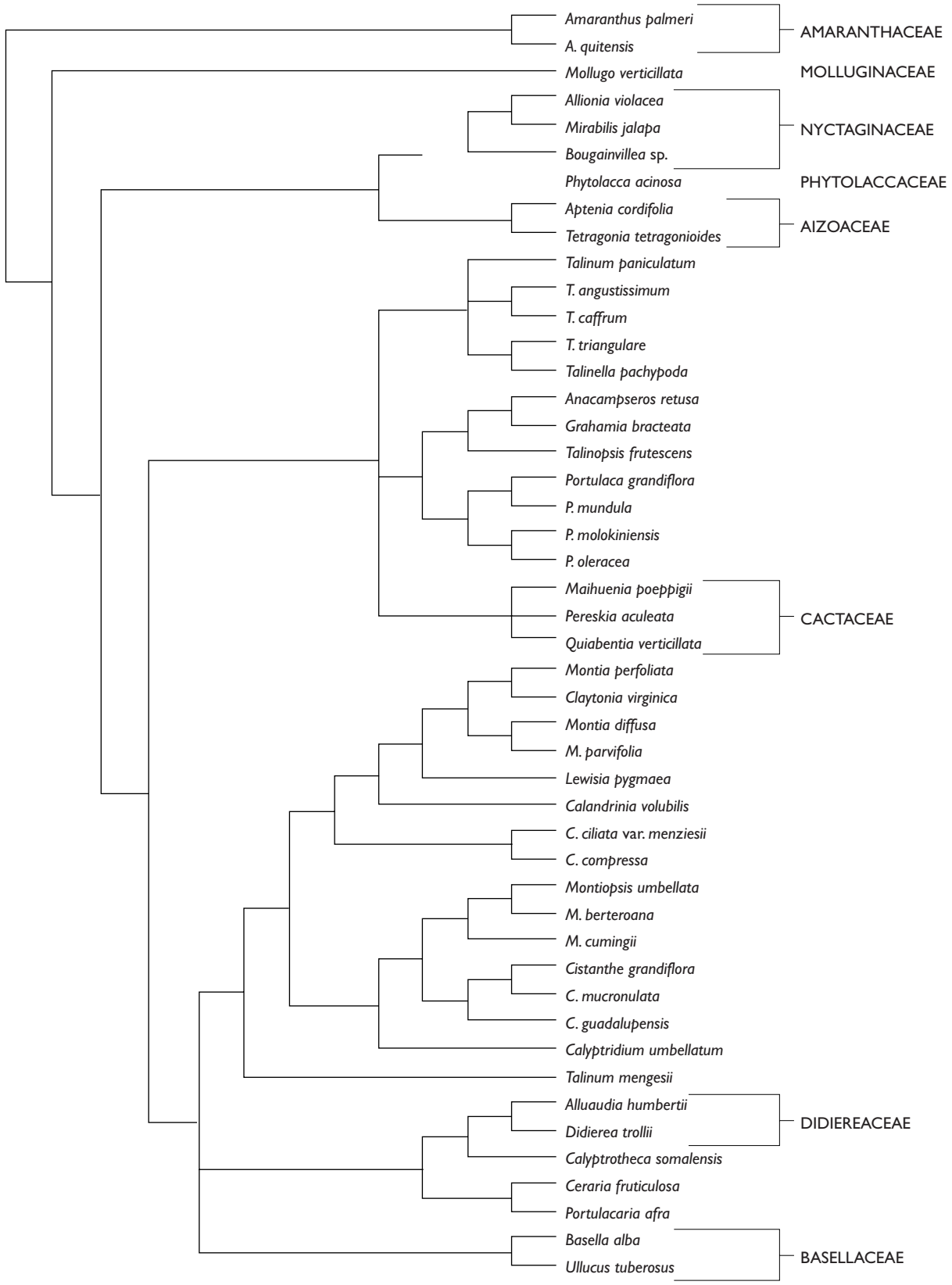


Figure 1.2. Strict consensus tree of equally parsimonious trees from analysis of the *ndh*F gene sequence for the portulacaceous alliance, which includes Cactaceae, Portulacaceae, Didiereaceae, and Basellaceae (after Appleqvist and Wallace 2000).

unresolved is whether investigators eventually will recognize more than one family of the cacti for this evolutionary branch.

Defining Subfamilies of Cactaceae

All recent familial classifications of Cactaceae have recognized three major clades, most commonly classified as subfamilies: Pereskioideae, Opuntioideae, and Cactoideae (Hunt and Taylor 1986, 1990; Gibson and Nobel 1986; Barthlott 1988; Barthlott and Hunt 1993). Each subfamily is distinguished by structural criteria, for which there are relatively clear discontinuities among these three clades.

Subfamily Pereskioideae has been defined essentially as the pool of extant cacti with the primitive vegetative and reproductive features (Buxbaum 1950; Boke 1954; Bailey 1960; Gibson 1976; Gibson and Nobel 1986). As traditionally defined, this subfamily has no known structural synapomorphy (Barthlott and Hunt 1993). Two genera have been assigned to this subfamily: *Pereskia* (16 spp.; Leuenberger 1986) and the Patagonian *Maihuenia* (2 spp.; Gibson 1977b; Leuenberger 1997). The broad-leaved shrubs and trees of *Pereskia* and small-leaved, mound-forming plants of *Maihuenia* have totally different external vegetative morphology and anatomy but share some plesiomorphic (primitive) reproductive features (Buxbaum 1953). Vegetative morphology of *Maihuenia* grades into low-growth forms of Opuntioideae. In fact, both species of *Maihuenia* were originally described as species of *Opuntia* (Leuenberger 1997).

Subfamily Opuntioideae is the most easily defined by its structural synapomorphies: (1) areoles have glochids, i.e., very short and fine deciduous leaf spines that have retrorse barbs and are easily dislodged; (2) every cell comprising the outer cortical layer of the stem possesses a large druse, i.e., an aggregate crystal of calcium oxalate (Bailey 1964; Gibson and Nobel 1986); (3) pollen grains are polyporate and possess peculiar microscopic exine features (Leuenberger 1976); (4) the seed is surrounded by a funicular envelope, often described as being an aril; and (5) special tracheids occurring in secondary xylem (wide-band tracheids of Mauseth 1993a, 1995; vascular tracheids of Bailey 1964, 1966 and Gibson 1977a, 1978) possess only annular secondary thickenings (Gibson and Nobel 1986). Other distinguishing features could be listed but are not true synapomorphies, i.e., derived character states within the family.

Subfamily Cactoideae is less easily delimited by synapomorphies. In fact, probably only one general form applies to all genera: namely, the stem is succulent and possesses a minute, often microscopic, upper leaf (*Oberblatt*) subtending each areole (Boke 1944). This contrasts with Opuntioideae, in which the leaf is usually small, terete, succulent, and easily discernible to the unaided eye. In most species of the subfamily, stems of Cactoideae have ribs (tubercles and areoles are arranged in a vertical series), but this cannot qualify as a synapomorphy and would ignore the presence of stem ribs of certain Opuntioideae, especially corynopuntias (*Grusonia*). Nonetheless, among extant cacti, there are no apparent morphological stages linking the leafy, nonsucculent, aerole-bearing shoots of *Pereskia* to any of the suggested primitive ribbed forms of Cactoideae. Other features that clearly differentiate between leafy pereskias and plesiomorphic Cactoideae, such as an outer stem cortex consisting of multiseriate hypodermis, are also found in Opuntioideae.

New evidence to evaluate the commonly used subfamilial classification of Cactaceae comes from analyses of cpDNA structural arrangements of the chloroplast genome adjacent to the region of the *rbc*L gene and comparative sequencing of a number of plastid coding and noncoding sequences. Opuntioideae are clearly demarcated molecularly by the deletion of the gene *acc*D (ORF 512) in the plastid genome (Wallace 1995). All Cactoideae examined to date have a different deletion at the 5' end of the *acc*D region and have lost the intron to the plastid gene *rpo*C1, a deletion of approximately 740 bp, which supports a common ancestry for all members of this subfamily (Wallace 1995; Wallace and Cota 1996). The clades defined by these structural rearrangements are further supported by phylogenies determined from comparative sequencing.

Unfortunately, a unique genetic synapomorphy has not yet been discovered for subfamily Pereskioideae, as previously circumscribed, but *Pereskia* and *Maihuenia* are themselves divergent because they have not been found to share restriction site changes, although many occur uniquely as synapomorphies for each genus (Wallace 1995). In fact, nucleotide sequencing data now demonstrate that *Pereskia* and *Maihuenia* are as divergent from one another as either is from Opuntioideae and Cactoideae.

Wallace (2002) used nucleotide sequence data as justification to propose recognizing a fourth subfamily, Maihuenioideae. When recognized as a separate subfamily, Maihuenioideae have distinctive structural synapomorphies, including curious anatomical features within leaves not known to occur elsewhere in Cactaceae (Gibson 1977b; Leuenberger 1997). Wood features of *Maihuenia* are also diagnostic to a specialist (Gibson 1977b), although all the cell types found in *Maihuenia,* including the special

spindle-shaped tracheids with helical secondary thickenings, are also observed within other members of Cactoideae that have small growth forms (Gibson 1973; Gibson and Nobel 1986; Mauseth 1995; Mauseth et al. 1995; Mauseth and Plemons 1995).

The proposal by Wallace to recognize subfamily Maihuenioideae was discussed openly for five years in deliberations and correspondence with Cactaceae specialists of the International Organization for Succulent Plant Study (IOS). The Cactaceae Working Party of the IOS concentrated its efforts on clarifying infrafamilial relationships among species and genera and stabilizing nomenclature for the cactus family, in order to make informed decisions about revising its classification. This procedure, not protected by the current international code of nomenclature, should become an accepted practice of the systematic community, instead of using preliminary publications to justify scientific decisions. It may also become a standard practice in the future to include molecular systematic studies or cladistic analyses of morphological or molecular data as part of publishing a new plant species. In this regard, full subfamilial diagnoses can be found for the Opuntioideae and Cactoideae in Barthlott and Hunt (1993), for the Maihuenioideae in Wallace (2002, after Leuenberger 1997), and for the Pereskioideae, based on the diagnosis of *Pereskia* in Leuenberger (1986).

Transitions from Structural Analyses to Molecular Systematics

The 250-year history of cactus taxonomy and systematics, as in all plant families, was dominated by the use of structural characters to assign species to genera. Unfortunately, examples of evolutionary convergence and parallelism in cactus structure are commonly observed (Table 1.1). These include reversals in character states and neoteny, i.e., reversals to juvenile features. Losses of distinguishing taxon-specific features are certainly commonplace in this family, in which plant habit, stem morphology, stem anatomy, and flower characters have been targets of natural selection (Buxbaum 1950, 1953; Gibson 1973; Gibson and Nobel 1986; Barthlott and Hunt 1993; Cornejo and Simpson 1997). What now worries cactus systematists are the unrecognized cases of parallel evolution still hidden among the genera, where a feature has been relied on as being conservative but now is discovered not to be. Experts of a group can sharply disagree on assigning a species to one genus or another based on one individual emphasizing seed characters, one flowers, and another areoles or internal anatomy. One of these characters—or none—may hold the key to its real phylogeny, but which one?

Needed is a technique that is independent of structure, where cases of parallelism and convergence can be clearly recognized so that each species can be inserted into its proper phylogenetic lineage. Application of molecular systematic techniques to address these issues provides a fresh look at old problems. The goal of modern plant systematics is to obtain, for each family, an entirely new and potentially unbiased data set in which to test all presumed classifications.

Molecular Systematics of Cactoideae

As of January 1, 2000, sequences for several plastid DNA regions (*rbc*L, *rpl16* intron, *trn*L-F intergenic spacer, *ndh*F) for representative taxa within the Cactaceae have been completed at Iowa State University (R. S. Wallace and coworkers) and form the framework for phylogenetic comparisons of the various evolutionarily related groups within the family. Genomic DNA samples have been isolated from photosynthetic stems (and leaves, when available) representing all key species groups, including currently recognized genera, infrageneric taxa, and morphologically anomalous species for which assignment to a genus has been problematic. From the relatively small sample studied, many systematic tangles are becoming unraveled each time new groups are carefully sampled and analyzed. Even so, Cactaceae must be more thoroughly subsampled, and the task of processing hundreds of species is time consuming. Fortunately, molecular studies are no longer as costly as they were a decade ago, due to advances in sequencing technology. As the various evolutionary groups within the Cactaceae are sampled more intensively, more robust phylogenies will emerge to provide a more certain assessment of relationships within and among the subfamilies, tribes, and genera that constitute the family.

Results from future studies of molecular variation likely will be, as they have already been, very illuminating in Cactaceae. New data can also be somewhat disturbing in cases where it is learned how incorrect some previous taxonomic placements were. These earlier classifications mislead cactus systematists in attempts at classifying the family and establishing scenarios for its evolutionary changes. Findings from molecular studies have shown how difficult it is to estimate affinities among cacti by using only external or internal structural features. In practice, a combination of molecular and morphological data will serve to provide the best estimate of phylogeny within the Cactaceae and will assist taxonomists in producing a classification that incorporates evolutionary relationships in its hierarchies, while establishing a usable and practical classification.

TABLE 1.1
Examples of parallel and convergent evolution of features within Cactaceae, using examples from North and South America

	Taxon	
Feature	*North America*	*South America*
Growth habit and wood anatomy		
Creeping (procumbent) columnar	*Stenocereus eruca*	*Echinopsis coquimbanus*
Living rocks	*Ariocarpus fissuratus*	*Neoporteria glabrescens*
	Lophophora williamsii	*Oreocereus madisorianus*
Massive barrel	*Echinocactus ingens*	*Eriosyce ceratistes*
Cylindrical barrel	*Ferocactus wislizenii*	*Denmoza rhodacantha*
	Astrophytum myriostigma	*Copiapoa cinerea*
Two-ribbed epiphyte	*Disocactus biformis*	*Rhipsalis rhombea*
Resupinate epiphyte	*Selenicereus testudo*	*Pseudorhipsalis amazonicus*
Lateral cephalium	*Cephalocereus senilis*	*Espostoa lanata*
Epidermal papillae on green stem	*Peniocereus marianus*	*Pterocactus kuntzei*
	Opuntia pilifera	*Tephrocactus auriculatus*
Tubular red, hummingbird-pollinated flowers		
Shrubs	*Stenocereus alamosensis*	*Cleistocactus strausii*
Epiphytes	*Disocactus macdougallii*	*Schlumbergera truncata*
Hummingbird flowers with red to brown pollen	*Echinocereus triglochidiatus*	*Cleistocactus brookei*
	Mammillaria poselgeri	*Denmoza rhodacantha*
Hawkmoth flowers, white, nocturnal with long tube	*Epiphyllum phyllanthus*	*Selenicereus wittii*
Very small flowers	*Pseudorhipsalis* spp.	*Rhipsalis* spp.
More than one flower per areole	*Myrtillocactus cochal*	*Pseudorhipsalis amazonicus*
Dark, glandular areolar trichomes	*Stenocereus thurberi*	*Pilosocereus aurisetum*
Hydrochorous (floating) seeds with large hilum cup	*Astrophytum capricorne*	*Frailea phenodisca*
Small seeds with large arillate strophiole	*Strombocactus disciformis*	*Blossfeldia liliputana*
Mescaline	*Lophophora williamsii*	*Echinopsis pachenoi*
	Stenocereus eruca	
Large calcium oxalate druses in outer cortex of stem	*Opuntia basilaris*	*Monvillea spegazzini*
	Aztekium ritteri	

References: Buxbaum (1950, 1955); Gibson (1973, 1988a,b); Rowley (1976); Bregman (1988, 1992); Rose and Barthlott (1994); Zappi (1994); Barthlott and Porembski (1996); Porembski (1996); Barthlott et al. (1997).

Identifying the Oldest Taxa

When doing any type of contemporary phylogenetic analysis, the researcher must include at least one species that has the presumed primitive features of the group being studied. For Cactaceae as a whole, this has been easy because the leaf-bearing species of *Pereskia* and *Maihuenia* are undisputed choices, and they are then assumed to have retained important plesiomorphic morphological or sequence characters for phylogenetic analyses. For Opuntioideae also, the choice is obvious with such leafy forms in the genera *Pereskiopsis, Quiabentia,* or *Austrocylindropuntia.* However, for subfamily Cactoideae and each of its tribes, making an a priori choice of taxa to best represent the primitive species has been a field of great speculation and, until now, selecting the primitive taxon has been a subjective process. Often, species possessing primitive features are not the ones widely cultivated or readily available; these groups typically inhabit inaccessible localities or sites where collection is not frequent and are usually incompletely described.

Buxbaum (1950) proposed that the primitive cereoid cactus would logically be one that had a woody form like a typical dicotyledon and relatively few ribs, e.g., in certain species of *Leptocereus.* Later, the tribe Leptocereeae (Buxbaum 1958) was often used as a taxonomic category to include cereoids having primitive vegetative and reproductive features. Out of that assemblage has emerged *Calymmanthium substerile* Ritter from northern Peru, which so far has served admirably as the outgroup for all phylogenetic analyses of cpDNA variation in subfamily Cactoideae (Fig. 1.3). In every molecular systematic study conducted on subfamily Cactoideae, *Calymmanthium* was found to be the most basal lineage in this group.

Calymmanthium is a poorly known columnar monotype. The few cultivated specimens exhibit juvenile shoots with basitonic branching, whereas, in nature, this species can achieve a height of 8 m (Backeberg 1976). Its solitary flower develops in a bizarre way, in that the lower portion is somewhat like a vegetative shoot with long, green scales, whereas the upper portion is more like the typical cereoid flower (Backeberg 1976). A liquid-preserved specimen of *C. substerile* collected in the wild by Paul Hutchison (3567, with J. K. Wright, January 1964; UCB jar 1000) is stored at the University of California, Berkeley, herbarium. This specimen has seven ribs, whereas juvenile shoots tend to have only three or four (Backeberg 1962, 1976). This species has simple stem anatomy, with an unremarkable epidermis, a uniseriate to biseriate collenchymatous hypodermis with relatively thin walls, and no mucilage cells in either cortex or pith.

When compared with other columnar cacti using molecular data, *Calymmanthium* lacks many of the synapomorphic nucleotide substitutions seen in the other tribal groups. Based on the plastid DNA sequences studied to date, it does not ally with either tribe Leptocereeae or Browningieae, where it has been placed in previous taxonomic treatments, nor does it fall within the clade of the predominantly South American columnar cacti of tribes Cereeae or Trichocereeae. Indeed, *C. substerile* may be the only remaining representative of a cactus lineage that most closely represents the ancestral form of subfamily Cactoideae.

There may be other, yet unstudied species that are also plesiomorphic, relative to the majority of cacti in the subfamily, and would join *C. substerile* as "primitive outlier" taxa. Other cacti showing little morphological differentiation from *Calymmanthium* are often considered "primitive" in the tribes to which they are associated (e.g., *Corryocactus* [including *Erdisia*], *Lepismium* [including *Pfeiffera* and *Lymanbensonia*], and *Leptocereus*). Future molecular studies will continue to elucidate the positions of the most primitive members of the Cactoideae and will add more systematic information to evaluate the position of *Calymmanthium* and its placement as the basal lineage of the subfamily.

Epiphytic Cacti

Nearly 130 epiphytic species of Cactaceae are found in the neotropical forests and woodlands. *Disocactus* (including *Nopalxochia*), *Pseudorhipsalis, Epiphyllum, Rhipsalis, Hatiora,* and *Schlumbergera* are genera mainly of holoepiphytes, i.e., true epiphytes and epiliths that do not root in soil. *Hylocereus* (including *Wilmattea*) and *Selenicereus* include numerous species that are facultative epiphytes or secondary hemiepiphytes, initially rooting in soil, and later becoming fully epiphytic.

Epiphytic cacti arose from ribbed, terrestrial columnar cacti. This was an obvious conclusion by early students and collectors of cacti, and no one has ever suggested the reverse, because epiphytes are too highly specialized to have given rise to the larger terrestrial cacti. Several major shifts in structure from terrestrial to epiphytic life have been hypothesized:

1. Epiphytes easily form adventitious roots along the stem and use these roots to anchor themselves to bark or rocks, as well as to absorb water and minerals. Many cacti have the ability to form adventitious roots from stem tissues, but holoepiphytes and hemiepiphytes do so while the stems are still attached to the host plant.

2. Stems of many cactus holoepiphytes are broad and leaflike, possessing a high surface-to-volume ratio (Sajeva and Mauseth 1991). The ribs of holoepiphytes are thinner than ribs of terrestrial cacti, not providing enough bulk to support an upright plant and requiring the plant to live in wetter habitats because the stem does not store much water for periods of drought. Holoepiphytes with very thin, two-ribbed stems often do not possess a collenchymatous hypodermis (e.g., in *Schlumbergera, Disocactus,* and *Epiphyllum*), whereas multiribbed columnar stems always form this support tissue (Gibson and Horak 1978).

3. Wood development is scanty, and the woody cylinder is very narrow, yielding a very thin and nonsucculent pith. Therefore, this wood is not used to support the plant, and the pith is not designed to store water for dry seasons.

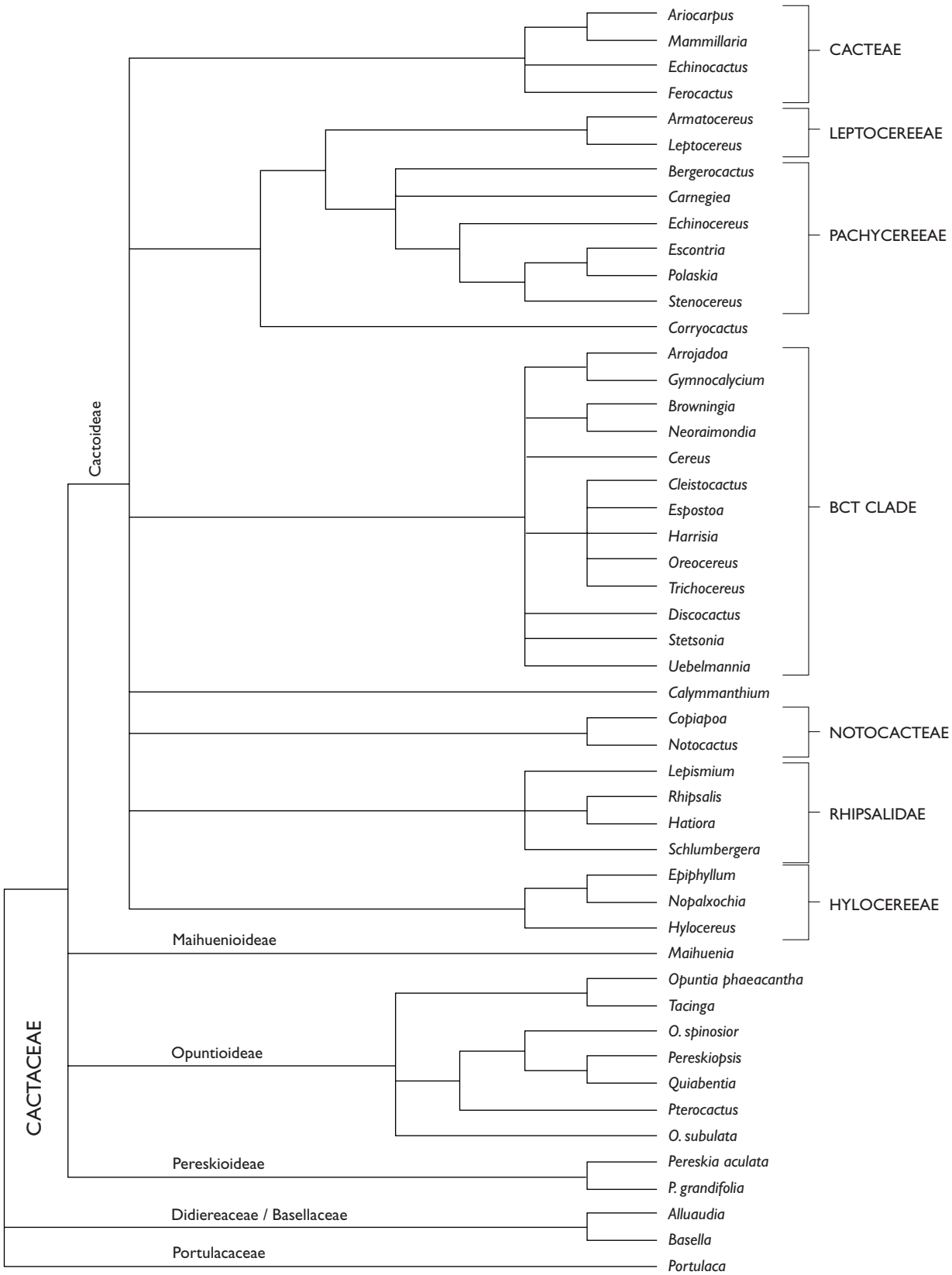


Figure 1.3. Strict consensus tree of 22,400 equally parsimonious trees from analysis of the *rbc*L gene for the family Cactaceae. A total of 1,434 bp of sequence was used for comparisons. Some important nodes in this tree are still unresolved.

4. Spination on stems of cactus epiphytes, especially on adult shoots, has been highly reduced or totally eliminated. One might expect that these cacti lack spines because hanging plants are not easily eaten by mammals, but the most likely explanation is that spines have been lost because they block sunlight from reaching the photosynthetic tissues of the stem (Gibson and Nobel 1986).

Cactus epiphytes are classified within two different tribes, the primarily South American Rhipsalideae and the primarily North American Hylocereeae, implying that within Cactoideae epiphytism evolved independently at least twice from terrestrial, ribbed columnar cacti, i.e., on each of the continents (Gibson and Nobel 1986; Barthlott 1987). The speculation has been that Rhipsalideae evolved from ancestors like *Corryocactus* (Barthlott 1988) in western South America, passing through transitional forms resembling *Lepismium* enroute to *Rhipsalis, Schlumbergera,* and *Hatiora,* which inhabit the major center of diversity for this tribe in Brazil. In North America, especially Central America and the West Indies, shrubby species of Hylocereeae, with arching stems and scandent growth habits, would have been the ancestors of climbing hemiepiphytes, e.g., *Hylocereus* and *Selenicereus,* as well as the highly specialized two-ribbed, spineless holoepiphytes of that tribe.

Molecular techniques have led to an important revelation. The tribes with epiphytes likely represent two of the basal (i.e., the earliest divergent) lineages of subfamily Cactoideae. Based on cladistic analysis of the chloroplast-encoded gene *rbc*L, hylocereoid epiphytes of *Disocactus* (subgenus *Aporocactus*), *Epiphyllum,* and *Hylocereus,* as well as hemiepiphytes of *Selenicereus,* appear to have diverged as a distinct lineage before, for example, *Leptocereus* and *Acanthocereus* (Wallace 1995; Cota and Wallace 1996), and prior to the divergence of most columnar and barrel cactus lineages.

Early divergence of epiphytic groups from the columnar and barrel forms suggests that there was a rapid evolutionary radiation that occurred within subfamily Cactoideae. The hypothesized rapid radiation is likely the reason for the lack of resolution (common occurrence of polytomy) among the major tribal lineages of subfamily Cactoideae. Until further studies of molecular variation are complete—using additional DNA markers and more intensive sampling—the true branching order of the Cactoideae phylogenetic tree will remain unresolved and in a "polytomy" state.

Columnar Cactus Lineages

Columnar cacti are presumably derived from a *Calymmanthium*-like ancestor that retained the upright, ribbed habit. Many columnar cacti are capable of supporting massive stems with their combined rib, parenchymal, and vascular structures (Cornejo and Simpson 1997). Molecular evidence currently suggests that there are two primary clades of columnar cacti that arose from the South American ancestral populations, each having inferred common ancestries (Fig. 1.3). The first clade comprises three former tribes that share a 300 bp deletion in Domain IV of the plastid *rpl*16 intron, strongly suggesting a common ancestry based on this unique loss of DNA. Members of the tribes Browningieae, Cereeae, and Trichocereeae all share this DNA deletion (R. S. Wallace, unpublished observations). Acknowledging here the limited molecular phylogenetic resolution found within this group of cacti to date, the cohort of genera found with this 300 bp deletion have been designated the "BCT" clade until more data are found to resolve the actual intertribal and intergeneric relationships. The members of the BCT clade show tremendous diversity in growth habit, size, and habitat preferences, and this clade is exemplary in its levels of floral morphological variation and suites of pollination types, including insect, bat, hawkmoth, and hummingbird syndromes. Interestingly, Buxbaum (1958) proposed that these groups are related to one another and constituted one major radiation in South American cacti. Based on the scaly nature of the perianth in members of tribe Browningieae, members of Cereeae and Trichocereeae are assumed to be more recently derived than those of Browningieae. This assumption needs to be checked with additional study and accompanying phylogenetic analysis.

Phylogeny of the North American columnar cacti is somewhat better understood (Gibson and Horak 1978; Gibson 1982; Gibson et al. 1986). Molecular data currently suggest that the two major lineages (tribes Leptocereeae and Pachycereeae) arose from a *Corryocactus*-like transitional form (derived from the original *Calymmanthium*-like ancestor in the northwestern Andes), and subsequently they radiated northward into North America within two geographic zones. In Central America and the Caribbean, Leptocereeae arose (*Leptocereus, Acanthocereus,* and *Dendrocereus*), achieving maximal diversity in the Greater Antilles, which formerly formed the backbone of Central America (Gibson and Nobel 1986). The phylogenetic sister taxon to the Leptocereeae is tribe Pachycereeae, identified as having two distinct evolutionary components

within it that are recognized taxonomically at the subtribe level (Pachycereinae and Stenocereinae of Gibson and Horak 1978; Gibson 1982; Cota and Wallace 1997). Numerous Pachycereeae and Leptocereeae may be characterized as having primarily bat pollination, although insect and hummingbird pollination are found in some taxa. Certain arborescent Pachycereeae form extensive woodlands in semiarid habitats throughout Mexico and other places and provide an excellent example of ecological parallelisms for the extensive woodlands of *Cereus, Echinopsis* (i.e., the Trichocerei), *Browningia,* and *Armatocereus* found in similar habitats of South America.

Cacteae and Notocacteae

Systematic studies of the tribe Cacteae have begun to elucidate the complex intergeneric relationships in this, the most speciose tribe of Cactoideae (Cota and Wallace 1997; Butterworth and Wallace 1999; Butterworth et al. 2002). Preliminary results reinforce the traditional hypothesis, e.g., that of Buxbaum (1950) or Barthlott (1988), that the ancestor of Cacteae probably was ribbed, and that the most highly derived taxa often have tubercular stem structures, as seen in *Coryphantha* and *Mammillaria.* This observation is not surprising per se, because one expects the barrel cacti with ribs to be derived from columnar cacti with ribs, and the barrel cacti of *Echinocactus* and *Ferocactus* have often been depicted as the basal taxa of the Cacteae. However, a number of interesting revelations about certain genera and their relationships are emerging from the molecular data that directly address questions of generic circumscription and monophyly. For example, as currently circumscribed, the genera *Ferocactus* and *Echinocactus* are paraphyletic or polyphyletic, and these species require further study to resolve the relationships as elucidated by morphological and molecular characters. One particularly surprising discovery originating from molecular studies is that the highly specialized plants of *Aztekium,* together with *Geohintonia,* represent the most primitive living lineages of Cacteae. This is an example where modern plants may manifest highly specialized features, but they may still be considered basal lineages when phylogenetic analyses of appropriate data are conducted.

Mammillaria, the largest genus of the Cactoideae with about 200 species, as currently treated, is monophyletic. The peculiar species *Oehmea beneckei* and *Mammilloydia candida* are clearly nested within *Mammillaria* and should not, therefore, be recognized as segregate genera. A close relationship between hummingbird-pollinated *Cochemiea* and *Mammillaria* also has been confirmed, although they are more distant than was previously thought. *Cochemiea* appears to be basal to *Mammillaria,* which may prompt systematists to recognize it as a segregate genus. Molecular systematic studies to evaluate the extensive infrageneric classification of *Mammillaria* also will determine whether the morphological variants identified by traditional taxonomists are supported by genetically based DNA variation and therefore will provide valuable insights into the speciation processes of recently diverged cactus groups. Future studies of additional genera in the Cacteae will contribute to a better understanding of phylogenetic radiation in Mexico and surrounding regions of this monophyletic tribe.

Tribe Notocacteae is the South American counterpart to Cacteae. This evolutionary branch includes a broad array of low-growing barrel cacti native to various areas of South America, including Chilean deserts, lowland grasslands of Argentina, southern Brazil, Paraguay, Uruguay, and related habitats. Although not as diverse as Cacteae, Notocacteae exhibit similar diversity in stem morphology, with short solitary or clumping barrel forms. The Notocacteae include genera such as *Blossfeldia, Copiapoa, Eriosyce* (including *Neochilenia, Neoporteria,* and *Pyrrhocactus*), *Notocactus, Parodia,* and perhaps *Eulychnia,* all strictly South American lineages and likely derived from ancestral populations arising farther north and west. Only limited molecular study of the Notocacteae has been conducted, so the intergeneric relationships of this tribe are still not well understood.

One central question to be resolved is whether the two "barrel cactus" tribes (Cacteae and Notocacteae) arose from a common ancestor during the early diversification of the Cactoideae. If these tribes are determined to be sister groups, the barrel cacti will then serve as a good example for independent morphological evolution along different paths on different continents that resulted in dissimilar morphological solutions to similar evolutionary and environmental challenges. Furthermore, a phylogeny for the Notocacteae could also shed light on the pattern of migration seen in southeastern South America, as well as establish evolutionary links of the isolated Atacama Desert species to those purportedly related genera on the eastern side of the Andes.

Solving Classification Problems Using Molecular Techniques

Data from cpDNA may also help cactus systematists to determine whether an oddball taxon should be treated as a monotypic genus or placed into another genus. Within subtribe Stenocereinae of the Pachycereeae occurs a mas-

sive candelabriform columnar cactus that Gibson (1991) found to be structurally very distinct and proposed recognition as a monotypic genus, *Isolatocereus* Backeberg. However, this segregate is most commonly treated within the genus *Stenocereus,* with which it shares synapomorphic silica bodies (Gibson and Horak 1978; Gibson et al. 1986). Both cpDNA restriction site data (Cota and Wallace 1997) and gene sequence data strongly support recognizing *I. dumortieri* as a monotype, basal to the tightly nested species of *Stenocereus* (Fig. 1.4; Wallace 1995). Recognition of *Isolatocereus* is also supported by a cladistic analysis based on structural features (Cornejo and Simpson 1997).

Another example of generic realignments that benefit from molecular systematic study is found in the genus *Harrisia* (incl. *Eriocereus* and *Roseocereus*). This primarily South American and Caribbean genus has previously been classified in tribe Hylocereeae (Gibson and Nobel 1986; Hunt and Taylor 1986) or in the Leptocereeae or Echinocereeae (Barthlott 1988; Hunt and Taylor 1990; Barthlott and Hunt 1993). Studies of its plastid sequences for the gene *rbc*L, the *trn*L–F intergenic spacer, and the *rpl*16 intron all indicate instead that this genus has its closest evolutionary affinities with members of the tribe Trichocereeae in the BCT clade. Axillary hairs in the floral bracts are a morphological synapomorphy for placement of *Harrisia* into this tribe. Furthermore, *Harrisia* shares the 300 bp deletion in Domain IV of the *rpl*16 intron observed in members of the BCT clade, which eliminates the possibility that *Harrisia* should be assigned to either the Leptocereeae or Echinocereeae, which do not possess this unique deletion. Thus, *Harrisia* may be confidently placed within the Trichocereeae of the BCT clade.

Similar types of taxonomic placement problems can also be resolved at the species level. A scandent, relatively thin-stemmed cactus originally described as *Mediocactus hahnianus* from Rio Apa, Brazil, was transferred to the genus *Harrisia* by Kimnach (1987) based on morphological similarities—particularly of the flower and stem—between this species and other members of *Harrisia.* A molecular systematic study of the interspecific relationships in *Harrisia* (Wallace 1997) found that *H. hahniana* did not fall within the well-supported *Harrisia* clade or with any species of *Mediocactus* or *Hylocereus* (tribe Hylocereeae) but allied strongly with members of the genera *Trichocereus* and *Echinopsis* (also members of tribe Trichocereeae). Using the comparative sequence data from the *rpl*16 intron that corroborated similarities of floral morphology, Wallace transferred *H. hahnianus* to the genus *Echinopsis,* now of the BCT clade.

Presence or absence of a major structural rearrangement is very useful in determining evolutionarily related groups of taxa. Occurrence of the 300 bp deletion in the intron of the plastid gene *rpl*16 is useful for including or excluding taxa thought to be related to that clade. For example, the columnar cactus *Stetsonia coryne* from Argentina may have its closest affinities with members of Cereeae (Gibson and Nobel 1986), not Leptocereeae (Barthlott and Hunt 1993); members of the latter tribe do not share this 300 bp deletion. Similarly, *Neoraimondia, Armatocereus,* and the Galápagos Archipelago–endemic *Jasminocereus thourarsii* have affinities with members of tribe Browningieae (Barthlott and Hunt 1993), not Leptocereeae (Gibson and Nobel 1986). Further study of these relationships will broaden the information base from which more robust hypotheses about columnar cactus evolution and migration in South America can be more reliably made.

Phylogenetic Studies of Subfamily Opuntioideae

Until very recently, most cactus systematists and hobbyist cactus growers had focused little attention on classification of the 250 species of Opuntioideae, or approximately 15% of the family. This is regrettable because some opuntias are dominant perennials in drylands of the New World or have become weedy invaders elsewhere and spread by grazing habits of livestock (Nobel 1994, 1998). Important food sources are obtained from platyopuntias (Russell and Felker 1987). Understandably, gardeners generally elected not to cultivate opuntias, which have nasty, irritating glochids and are not easily controlled plants, but now, growing small opuntioids, especially taxa from western South America, has become very popular among cactus enthusiasts.

Due to the relatively small amount of systematic research emphasis placed on the Opuntioideae by past researchers, a significant gap exists in our understanding of the evolutionary relationships among these members of the Cactaceae. Perhaps most important, an intensive phylogenetic analysis for this subfamily is required to evaluate the generic circumscription. Cactus researchers especially need to elucidate the early divergences of the opuntioid taxa to understand how many distinct lineages have resulted in North and South America, as well as what the generic "boundaries" are for genera and subgenera. For example, the relationships of the low-growth forms, such as in the genera *Maihueniopsis* and *Tephrocactus,* have been extremely hard to predict on the basis of superficial examination of external characters, and the evolutionary history of structural transitions has been an area merely of speculation.

A number of morphological transitions have been hypothesized for the opuntioid lineages. Two in particular are

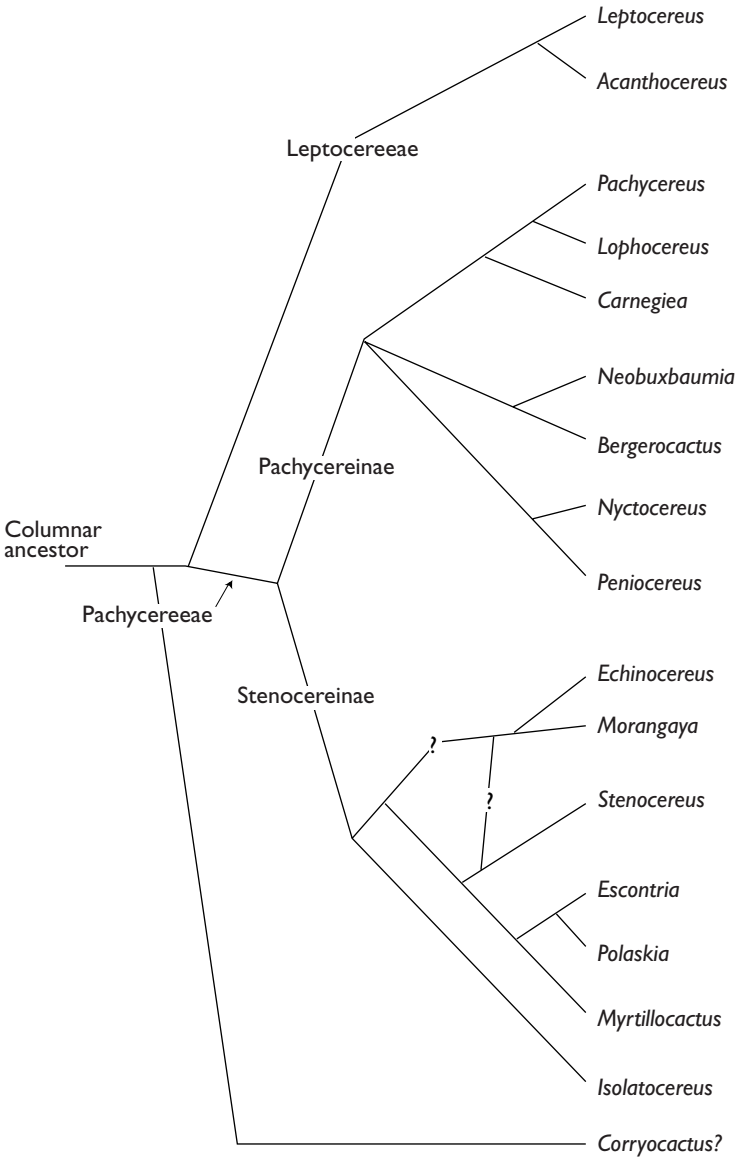


Figure 1.4. Hypothesized intergeneric relationships within some North American columnar cacti based on analyses of *rpl*16 intron sequences. Tribe Pachycereeae appears to consist of two subtribes, Stenocereinae and Pachycereinae (sensu Gibson and Horak 1978), but gene sequence analyses indicate that definitions of both subtribes need to be expanded to include other species.

key: (1) a shift from persistent leaves to ephemeral foliage leaves; and (2) changes in the shoot design from relatively uniform, cylindrical succulent stems to jointed stems with either cylindrical or flattened segments, i.e., cladodes (synonym, phylloclades). Another presumed trend has been a shift in growth habit from upright woody plants (shrubs to small trees) to shrubby or sprawling clumps, and even evolution of the geophytic habit in *Pterocactus,* in which most plant biomass is subterranean and the aboveground parts are annual shoots.

A factor that contributes considerably to the taxonomic confusion within the subfamily is the high level of phenotypic plasticity shown within many opuntioid taxa. In species with shoot features, different vegetative forms have at times been given different scientific binomials, adding to the nomenclatural problems of the group. Additionally, both polyploidy and hybridization have played a vital role in the evolution of the diversity of these cacti and have also contributed to nomenclatural chaos (Benson 1982). In fact, the Opuntioideae accounts for more than

75% of the polyploidy observed in the Cactaceae (Benson 1982).

Although Opuntioideae present a considerable challenge to the cactus systematist, recent studies have provided much insight into opuntioid evolution. Of critical importance is sharply defining the generic concept for the genus *Opuntia.* In some classifications, *Opuntia* represents a wide array of small terete-stemmed trees, shrubs, plants with dwarf and clump-forming habits, chollas, club chollas, platyopuntias (prickly pears), and the tree opuntias of Brazil and the Caribbean. In other classifications, these same plants may be reclassified into ten or more genera. Some morphologically distinct plants, such as the geophytic species of *Pterocactus* in Argentina or the persistent leaf-bearing species *Pereskiopsis* and *Quiabentia* of North and South America, respectively, are more readily distinguished as segregate genera. But even here, *Pereskiopsis* and *Quiabentia* have been lumped into a single genus (Hunt and Taylor 1990).

Studies of seed morphology and other aspects of micromorphology have provided evidence that a complete reevaluation of the generic circumscriptions in the subfamily is warranted (Stuppy 2002). Molecular systematic studies by Dickie (1998) and Dickie and Wallace (2001) were specifically designed to address these generic circumscription problems. From studies of plastid DNA variation (*rbc*L, *trn*L–F intergenic spacer, *rpl*16 intron), the inferred phylogeny indicated that there were five clades within the subfamily, related both geographically and morphologically (Fig. 1.5), which follows the structural evidence detailed by Stuppy (2002). A basal lineage for the subfamily appears to include the species referable to the genera *Austrocylindropuntia* and *Cumulopuntia,* both native to the Peru-Bolivia-Chile Andean regions. Other clades are the narrowly distributed South American *Pterocactus;* a clade of *Maihueniopsis-Tephrocactus* (including *Puna*); and two clades containing the more widely distributed opuntioids found in both North and South America. The first of these more diverse clades is the "cylindroid" lineage, showing a south to north grade of specialization from leafy, cylindrical-stemmed ancestral forms such as *Pereskiopsis* and *Quiabentia* of North and South America, respectively, to more specialized, segmented-stemmed chollas of North America (*Grusonia* [including *Marenopuntia, Micropuntia,* and *Corynopuntia*] and *Cylindropuntia*).

For the flat-stemmed opuntioid taxa, a similar but more subtle south-to-north transition is seen, beginning with the plesiomorphic genus *Miqueliopuntia* of the Atacama Desert. Here terete-stemmed, clump-forming opuntioids (in contrast to the solitary terete stems of *Austrocylindropuntia*) tend to grade into plants with flattened stems, as in *Airampoa,* which form the basal lineages of the platyopuntia clade. Forest emergents, such as in *Brasiliopuntia* and *Consolea* of Brazil and the Caribbean, respectively, also show morphological transitions from terete stems of their trunks to flattened leaflike phylloclades ("pads"). These stem joints are seasonally deciduous in *Brasiliopuntia.* The true platyopuntias (genus *Opuntia* in the type sense) have experienced complete loss of cylindrical stems, except in seedling stages. One notable exception in the caatinga of eastern Brazil is *Tacinga funalis,* a scrambling, thin-stemmed subshrub that has reverted to entirely terete stems, despite its clear affinities with flat-stemmed prickly pears, as determined by molecular data.

The taxonomic dilemma is that the majority of the genera discussed here have typically been subsumed into a "catch-all" genus, *Opuntia.* The molecular data have made it possible to determine evolutionarily related groups (e.g., five major clades) and has provided sufficient evolutionary information about these lineages to construct a robust phylogeny. The intergeneric groups defined by the molecular studies of Dickie and Wallace (2001) are essentially the same generic groups that Stuppy (2002) proposed based on studies of seed structures, in that both suggest that approximately 12 to 15 genera should be recognized as monophyletic units within the subfamily. Furthermore, the morphological discontinuities observed between these opuntioid genera are, in reality, greater than those now recognized between members of tribes in Cactoideae (e.g., the tribe Cacteae), whose generic distinctions have only rarely been questioned.

Opuntioideae, therefore, offer a critical test for cactus systematics. Many researchers, for convenience, would prefer to have fewer and larger genera, but many smaller genera may have to be recognized to represent the true evolutionary lineages. Whether all or none of these smaller, demonstrably monophyletic groups are recognized at the rank of genus, subtribes, or tribes by cactus systematists remains to be seen. Discussions will eventually resolve these questions and incorporate the available data and conclusions into a practical and generally accepted classification for the Opuntioideae. Without a reliable phylogeny to form the basis of systematic comparisons, such discussions and interpretations of morphological variation would be very problematic, if possible at all.

New Insights into Cactus Evolution

Structural Properties

Having even the current, crude phylogenetic knowledge from molecular systematic studies has provided new in-

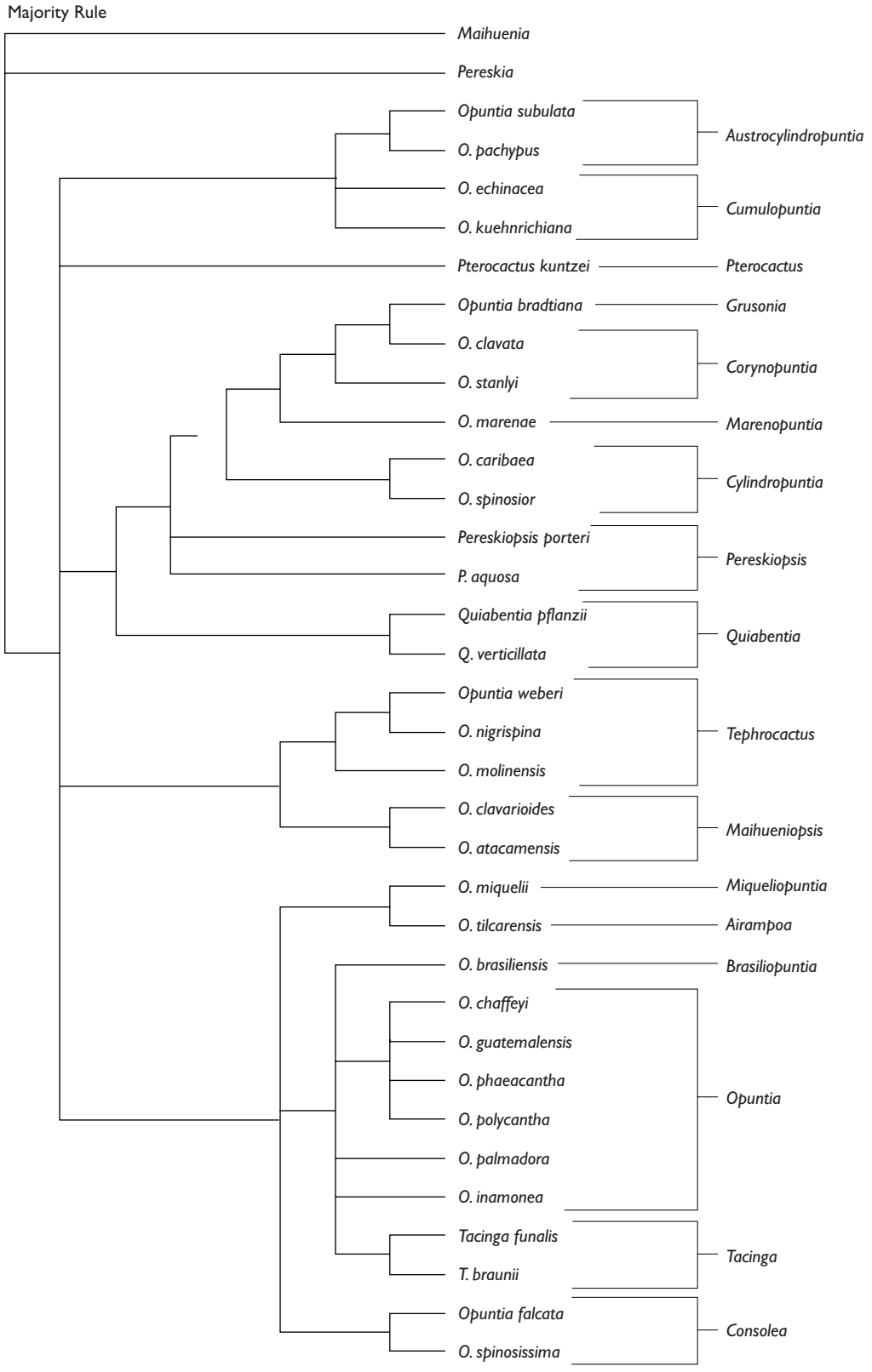


Figure 1.5. Strict consensus tree of 32,700 equally parsimonious trees from analysis of *rpl*16 intron sequences in the subfamily Opuntioideae (Dickey and Wallace 2000). The analysis strongly supports recognizing many of the segregate genera formerly proposed for opuntioids.

sight into how the structure of cacti has evolved. Perhaps gone will be the methods of using anatomical data to devise phylogenetic hypotheses. For example, Gibson and Horak (1978) used the presence of calcium oxalate crystals in the skin (epidermis and collenchymatous hypodermis) of the stem to indicate that certain species of Mexican columnar cacti are closely related and therefore not members of subtribe Stenocereinae (Pachycereeae). Some of the North American species possessing these calcium oxalate crystals were classified in the genus *Cephalocereus.* Zappi (1994) monographed the genus *Pilosocereus* (tribe Cereeae), which is greatly developed in Brazil, but which includes certain North America species of cephalocerei. The occurrence of such crystals (Fig. 1.6) now appears to be a shared primitive feature (symplesiomorphy) found in many of the basal taxa, e.g., Leptocereeae and Hylocereeae, as well as in subfamilies Opuntioideae and Cereeae (Gibson and Horak 1978; Mauseth and Ross 1988; Mauseth 1996; Mauseth et al. 1998). Therefore, presence of such crystals may instead be an ancient character of the Cactaceae. Furthermore, other Portulacineae have epidermal calcium oxalate features (Gibson 1994), suggesting an even older origin of that character, and probably indicating that crystals have been evolutionarily lost in a number of lineages. This permits researchers to determine where regulatory genes first arose to yield a character.

A phylogenetic reconstruction of Cactaceae will elucidate where features first evolved in cacti. For example, did the collenchymatous hypodermis typical of subfamilies Opuntioideae and Cactoideae evolve once from a common ancestor or twice independently? A medullary vascular system occurs in many, but not all, Cactoideae (Gibson and Horak 1978; Mauseth 1993b), and a molecular phylogeny may determine whether absence of medullary bundles in any species of the family is a primitive or a derived, lost character state. Narrow pith and absence of mucilage cells have been treated as primitive characters for cactus stems, and this can also be tested by character mapping on cladistic models.

Revised Biogeographic Models Based on Molecular Studies

Evolution of the cacti from ancestral populations of portulacaceous ancestors is being supported again and again by molecular studies of a variety of genes and other DNA sequences (Applequist and Wallace 2000). Previous hypotheses about the center of origin and dispersal of the Cactaceae have been reviewed (Gibson and Nobel 1986), but conflicting concepts remain as to whether the "northwest South America" hypothesis or the "Caribbean origin" hypothesis should prevail.

The family-wide studies of DNA variation, as well as more intensive studies in subfamilies and tribes, begin to converge on a single, different hypothesis that is consistent with the early Gondwanan ancestry of the families of the Caryophyllales, and that of paleoclimatic and paleogeologic activities in western South America. When the phylogenies are determined for each of the various major cactus clades investigated, the recurrent observation is that the basal groups, presumably representing the plesiomorphic lineages, today inhabit the central Andean region of northern Chile, northwest Argentina, Bolivia, and Peru. Of those relevant systematic studies completed on cactus taxa with representatives in this region, the plesiomorphic members are invariably found here. This is true for the genera *Pereskia, Harrisia,* and *Lepismium,* as well as for the tribe Rhipsalidae, the subfamily Opuntioideae (*Austrocylindropuntia* and *Cumulopuntia* basal), and the subfamily Cactoideae (*Calymmanthium* basal). Because the plesiomorphic taxa of presumably independent lineages (following divergence from a common ancestor) are still found in this general region, it is reasonable to assume that this represents the center of origin or earliest radiation for the Cactaceae. Other studies of South American flora (e.g., Raven and Axelrod 1974) cite the importance of this region as a source for diversification in numerous angiosperm lineages, noting the importance of the Andean orogeny in shaping the migration pathways of the resultant diverged lineages.

The proposed scenario for the origin and diversification of cacti begins with its divergence from *Portulaca*- or *Talinum*-like ancestors, perhaps in the Upper Cretaceous after the breakup of Gondwana and the isolation of South America from the remaining austral continents about 110 million years ago. Ancestral populations ultimately became more succulent and "stem-dominant," with a concomitant reduction in the importance of leaves as Crassulacean acid metabolism (Chapter 4) became the dominant photosynthetic pathway. As the major lineages (subfamilies) diverged, they also appear to have followed three main migration paths, one to the north, one to the south along the Andean Cordillera, and another from west to east to establish another center of diversification in eastern Brazil. Examples of southerly migrating groups are *Maihuenia, Pterocactus,* and members of tribes Trichocereeae and Notocacteae. Eastward migrants include members of tribes Rhipsalideae and Cereeae, *Harrisia,* and some Opuntioideae, notably *Brasiliopuntia* and the caatinga species of the *Opuntia inamoena* complex, including both species of *Tacinga.* Following a northward migration were a number of cylindrical opuntioid lineages arising from

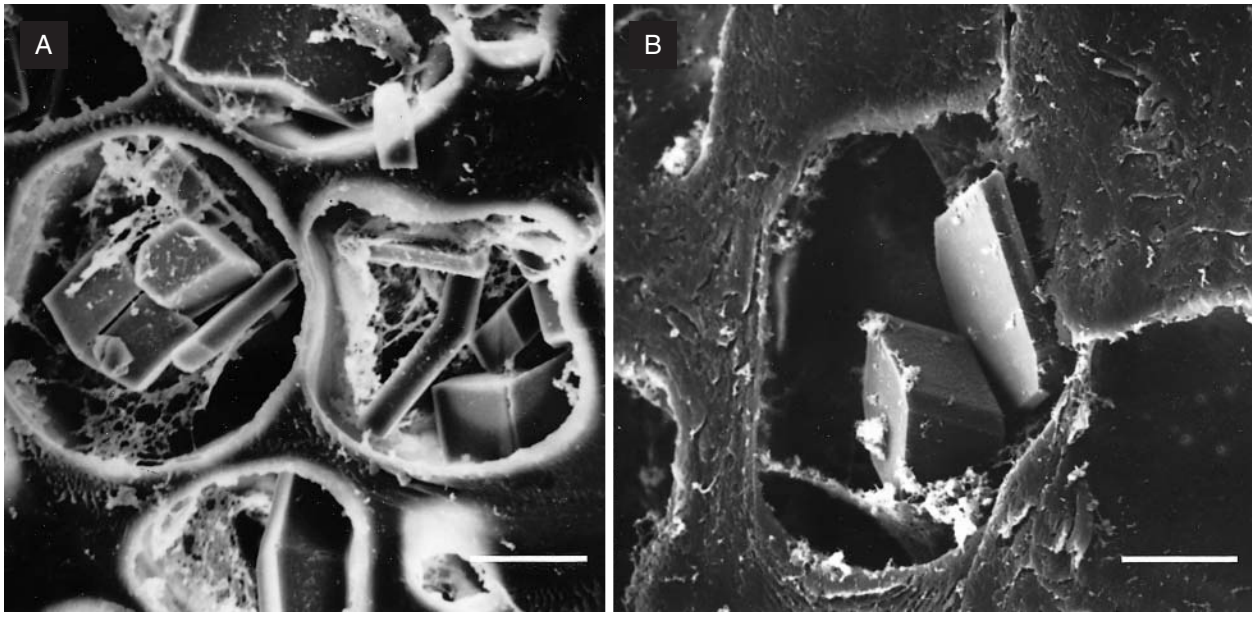


Figure 1.6. Scanning electron photomicrographs of calcium oxalate crystals in the skin of two columnar cacti: (A) *Mitrocereus fulviceps,* and (B) *Armatocereus laetus.* Scale bars = 10 µm.

Austrocylindropuntia and *Quiabentia,* resulting in divergences of the cholla lineages of North America (*Cylindropuntia* and *Grusonia*). A parallel situation also occurred in flat-stemmed *Opuntia* taxa, where the prickly pears (*Opuntia* sensu stricta) diversified on the mainland while the genus *Consolea* arose in the Caribbean.

In subfamily Cactoideae, three major lineages migrated north (presumably along the Andean corridor) until they reached Central America and the Caribbean islands (which were located much farther west of their present location). From what likely were *Corryocactus*-like ancestors, the divergence of tribes Pachycereeae (mainland) and Leptocereeae (Caribbean) occurred in this region (paralleling the *Opuntia* example above). The barrel-cactus forms seen in tribe Cacteae (predominantly mainland) radiated rapidly and migrated to inhabit a wide geographic range in North America, extending as far north as Canada. Epiphytic cacti of tribe Hylocereeae were under environmental constraints to inhabit more mesic habitats and thus remained in Central America and northern South America, limited by water availability and moderate temperature requirements.

The evolutionary scenario presented above is at least consistent with the paleogeographic conditions over the last 60 million years, and the relationships of the various cactus groups are supported by several independent studies of different groups of cacti and using different molecular markers. As more molecular and morphological data accrue from future studies of cactus evolution and systematics, the hypotheses presented here regarding the biogeographic history of the family may be further refined or even rejected. At present, these are the best working hypotheses for the origins of the various lineages within the family and why they are distributed in their present geographic patterns.

Concluding Remarks

The cactus community is composed of a great diversity of users, and most are keenly interested in classification below the level of the subfamily, needing correct binomials and the assignment of each species to the proper genus. Above all, there is a great need for stabilization of names in the Cactaceae (Hunt and Taylor 1986, 1990; Hunt 1991). At the same time, scientists absolutely require a phylogeny of the family so that applications can be made for understanding the evolution of characters and their various states, as well as understanding the processes of speciation, biogeographic radiation, and the evolution of cacti as host plants for other organisms.

Although a cladistic approach to classification may appear destabilizing at first, a much more stable system of classification should be produced soon. Questions about assigning a plant to a genus can become pro forma and inexpensive using genetic markers. It would not be unreasonable for the cactus community to require routine genetic testing of new taxa before publication to avoid

confusion produced from structural analyses. The major issue then confronting an author would be whether the population is assignable to a previously described species or is new to science.

Given the present understanding of the evolutionary patterns in the Cactaceae, considerable research is still needed to address questions of generic delimitation, tribal circumscription, and species identity. Integration of molecular, morphological, and biogeographic data will undoubtedly bring about a more robust and useful perspective on relationships within the Cactaceae and, to users of these data, a more stable and reliable source of biological information about this diverse and exceptional family.

Literature Cited

Angiosperm Phylogeny Group. 1998. An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* 85: 531–553.

Appleqvist, W. L., and R. S. Wallace. 2001. Phylogeny of the portulacaceous cohort based on *ndh*F gene sequence data. *Systematic Botany* 26: 406–419.

Backeberg, C. 1962. *Cactaceae,* Vol. 6. Gustav Fischer-Verlag, Jena, East Germany.

Backeberg, C. 1976. *Cactus Lexicon,* 3rd ed. Blandford Press, Poole, Dorset, United Kingdom.

Bailey, I. W. 1960. Comparative anatomy of the leaf-bearing Cactaceae. I. Foliar vasculature of *Pereskia, Pereskiopsis,* and *Quiabentia. Journal of the Arnold Arboretum* 41: 341–356.

Bailey, I. W. 1964. Comparative anatomy of the leaf-bearing Cactaceae. XI. The xylem of *Pereskiopsis* and *Quiabentia. Journal of the Arnold Arboretum* 45: 140–157.

Bailey, I. W. 1966. The significance of the reduction of vessels in the Cactaceae. *Journal of the Arnold Arboretum* 47: 288–292.

Barthlott, W. 1983. Biogeography and evolution in neo- and paleotropical Rhipsalinae. In *Dispersal and Distribution* (K. Kubitzki, ed.). Verlag Paul Parey, Hamburg, Germany. Pp. 241–248.

Barthlott, W. 1987. New names in Rhipsalidinae (Cactaceae). *Bradleya* 5: 97–100.

Barthlott, W. 1988. Über die systematischen Gliederungen der Cactaceae. *Beitrage Biologie der Pflanzen* 63: 17–40.

Barthlott, W., and D. R. Hunt. 1993. Cactaceae. In *The Families and Genera of Vascular Plants,* Vol. 2. (K. Kubitzki, J. G. Rohwer, and V. Bittrich, eds.). Springer-Verlag, Berlin. Pp. 161–197.

Barthlott, W., and S. Porembski. 1996. Ecology and morphology of *Blossfeldia liliputana* (Cactaceae): a poikilohydric and almost astomate succulent. *Botanica Acta* 109: 161–166.

Barthlott, W., S. Porembski, M. Kluge, J. Hopke, and L. Schmidt. 1997. *Selenicereus wittii* (Cactaceae): an epiphyte adapted to Amazonian Igapó inundation forests. *Plant Systematics and Evolution* 206: 175–185.

Behnke, H.-D. 1976a. Die Siebelement Plastiden der Caryophyllaceae, eine weitere spezifische Form der P-Typ Plastiden bei Centrospermen. *Botanische Jahrbücher für Systematik* 95: 327–333.

Behnke, H.-D. 1976b. Ultrastructure of sieve-element plastids in Caryophyllales (Centrospermae), evidence for the delimitation and classification of the order. *Plant Systematics and Evolution* 126: 31–54.

Behnke, H.-D. 1994. Sieve-element plastids. In *Caryophyllales: Evolution and Systematics* (H.-D. Behnke and T. J. Mabry, eds.). Springer-Verlag, Heidelberg, Germany. Pp. 87–121.

Benson, L. 1982. *The Cacti of the United States and Canada.* Stanford University Press, Stanford, California.

Boke, N. H. 1944. Histogenesis of the leaf and areole in *Opuntia cylindrica. American Journal of Botany* 31: 299–316.

Boke, N. H. 1954. Organogenesis of the vegetative shoot in *Pereskia. American Journal of Botany* 41: 619–637.

Bregman, R. 1988. Forms of seed dispersal in Cactaceae. *Acta Botanica Neerlandica* 37: 395–402.

Bregman, R. 1992. Seed studies in the subtribe Borzicactinae Buxbaum (Cactaceae); morphology, taxonomy, phylogeny and biogeography. *Botanische Jahrbücher für Systematik* 114: 201–250.

Butterworth, C. A., and R. S. Wallace. 1999. Phylogenetic studies of the tribe Cacteae. *Cactaceae Consensus Initiatives* 8: 7–9.

Butterworth, C. A., J. H. Cota-Sanchez, and R. S. Wallace. 2002. Molecular systematics of Tribe Cacteae (Cactaceae: Cactoideae): A phylogeny based on *rpl16* intron sequence variation. *Systematic Botany* (in press).

Buxbaum, F. 1950. *Morphology of Cacti. Section I. Roots and stems.* Abbey Garden Press, Pasadena, California.

Buxbaum, F. 1953. *Morphology of Cacti. Section II. The Flower.* Abbey Garden Press, Pasadena, California.

Buxbaum, F. 1955. *Morphology of Cacti. Section III. Fruits and Seeds.* Abbey Garden Press, Pasadena, California.

Buxbaum, F. 1958. The phylogenetic division of the subfamily Cereoideae, Cactaceae. *Madroño* 14: 177–206.

Buxbaum, F. 1966. The origin of the tribe Browningieae. *Cactus and Succulent Journal (U.S.)* 38: 43–46.

Clements, J. S., T. J. Mabry, H. Wyler, and A. S. Dreiding. 1994. Chemical review and evolutionary significance of the betalains. In *Caryophyllales: Evolution and Systematics* (H.-D. Behnke and T. J. Mabry, eds.). Springer-Verlag, Heidelberg, Germany. Pp. 247–261.

Cornejo, D. O., and B. B. Simpson. 1997. Analysis of form and function in North American columnar cacti (tribe Pachycereeae). *American Journal of Botany* 84: 1482–1501.

Cota, J. H., and R. S. Wallace. 1996. La citologia y la sistematica molecular en la familia Cactaceae. *Cactáceas y Suculentas Mexicanas* 41: 27–44.

Cota, J. H., and R. S. Wallace. 1997. Chloroplast DNA evidence for divergence in *Ferocactus* and its relationships to North American columnar cacti (Cactaceae: Cactoideae). *Systematic Botany* 22: 529–542.

Cronquist, A. 1981. *An Integrated System of Classification of Flowering Plants.* Columbia University Press, New York.

Cronquist, A., and R. F. Thorne. 1994. Nomenclature and taxonomic history. In *Caryophyllales: Evolution and Systematics* (H.-D. Behnke and T. J. Mabry, eds.). Springer-Verlag, Heidelberg, Germany. Pp. 5–25.

Dickie, S. L. 1998. Phylogeny and evolution in the subfamily Opuntioideae (Cactaceae). Master's Thesis, Iowa State University, Ames.

Dickie, S. L., and R. S. Wallace. 2001. Phylogeny and evolution in the subfamily Opuntioideae (Cactaceae): insights from *rpl16* intron sequence variation. *Systematic Botany* (in review).

Downie, S. R., and J. D. Palmer. 1993. A chloroplast DNA phylogeny of the Caryophyllales based on structural and inverted repeat restriction site variation. *Systematic Botany* 19: 236–252.

Downie, S. R., and J. D. Palmer. 1994. Phylogenetic relationships using restriction site variation of the chloroplast DNA inverted repeater. In *Caryophyllales: Evolution and Systematics* (H.-D. Behnke and T. J. Mabry, eds.). Springer-Verlag, Heidelberg, Germany. Pp. 223–233.

Downie, S. R., D. S. Katz-Downie, and K.-J. Cho. 1997. Relationships in the Caryophyllales as suggested by phylogenetic analyses of partial chloroplast DNA ORF2280 homolog sequences. *American Journal of Botany* 84: 253–273.

Eichler, A. W. 1878. *Blümendiagramme,* Part 2. Engelmann, Leipzig, East Germany.

Gibson, A. C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). *Biotropica* 5: 29–65.

Gibson, A. C. 1976. Vascular organization of shoots of Cactaceae. I. Development and morphology of primary vasculature in Pereskioideae and Opuntioideae. *American Journal of Botany* 63: 414–426.

Gibson, A. C. 1977a. Wood anatomy of opuntias with cylindrical to globular stems. *Botanical Gazette* 138: 334–351.

Gibson, A. C. 1977b. Vegetative anatomy of *Maihuenia* (Cactaceae) with some theoretical discussions of ontogenetic changes in xylem cell types. *Bulletin of the Torrey Botanical Club* 104: 35–48.

Gibson, A. C. 1978. Wood anatomy of platyopuntias. *Aliso* 9: 279–303.

Gibson, A. C. 1982. Phylogenetic relationships of Pachycereeae. In *Ecological Genetics and Evolution. The Cactus-Yeast-*Drosophila *Model System* (J. S. F. Barker and W. T. Starmer, eds.). Academic Press, Sydney. Pp. 3–16.

Gibson, A. C. 1988a. The systematics and evolution of subtribe Stenocereinae. 3. *Myrtillocactus. Cactus and Succulent Journal (U.S.)* 60: 109–116.

Gibson, A. C. 1988b. The systematics and evolution of subtribe Stenocereinae. 5. Cina and its relatives. *Cactus and Succulent Journal (U.S.)* 60: 283–288.

Gibson, A. C. 1991. The systematics and evolution of subtribe Stenocereinae. 11. *Stenocereus dumortieri* versus *Isolatocereus dumortieri. Cactus and Succulent Journal (U.S.)* 63: 184–190.

Gibson, A. C. 1994. Vascular tissues. In *Caryophyllales: Evolution and Systematics* (H.-D. Behnke and T. J. Mabry, eds.). Springer-Verlag, Heidelberg, Germany. Pp. 45–74.

Gibson, A. C., and K. E. Horak. 1978. Systematic anatomy and phylogeny of Mexican columnar cacti. *Annals of the Missouri Botanical Garden* 65: 999–1057.

Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer.* Harvard University Press, Cambridge, Massachusetts.

Gibson, A. C., K. C. Spencer, R. Bajaj, and J. L. McLaughlin. 1986. The ever-changing landscape of cactus systematics. *Annals of the Missouri Botanical Garden* 73: 532–555.

Hershkovitz, M. A. 1991. Leaf morphology of *Cistanthe* Spach (Portulacaceae). *Annals of the Missouri Botanical Garden* 78: 1022–1060.

Hershkovitz, M. A., and E. A. Zimmer. 1997. On the evolutionary origins of the cacti. *Taxon* 46: 217–232.

Hunt, D. R. 1991. Stabilization of names in succulent plants. *Regnum Vegetabile* 123: 151–155.

Hunt, D. R., and N. P. Taylor (eds.). 1986. The genera of Cactaceae: towards a new consensus. *Bradleya* 4: 65–78.

Hunt, D. R., and N. P. Taylor (eds.). 1990. The genera of Cactaceae: progress towards consensus. *Bradleya* 8: 85–107.

Kiesling, R. 1988. Cactaceae. In *Flora Patagónica 5, Dicotiledoneas dialipétalas (Oxalidaceae a Cornaceae)* (M. N. Correa, ed.). Coleccion Científica del INTA 8, Buenos Aires, Argentina. Pp. 218–243.

Kimnach, M. 1987. *Harrisia hahniana. Cactus and Succulent Journal (U.S.)* 59: 59–62.

Leuenberger, B. E. 1976. Die Pollenmorphologie der Cactaceae und ihre Bedeutung für die Systematik mit Berträgen zur Methodik rasterelektronenmikroskopischer. *Dissertationes Botanicae* 31: 1–321.

Leuenberger, B. E. 1986. *Pereskia* (Cactaceae). *Memoirs of the New York Botanical Garden* 41: 1–141.

Leuenberger, B. E. 1997. *Maihuenia*—monograph of a Patagonian genus of Cactaceae. *Botanische Jahrbücher für Systematik* 119: 1–92.

Mabry, T. J. 1964. The betacyanins, a new class of red-violet pigments, and their phylogenetic significance. In *Taxonomic Biochemistry and Serology* (C. A. Leone, ed.). Ronald Press, New York. Pp. 239–254.

Manhart, J. R. and J. H. Rettig. 1994. Gene sequence data. In *Caryophyllales: Evolution and Systematics* (H.-D. Behnke and T. J. Mabry, eds.). Springer-Verlag, Heidelberg, Germany. Pp. 235–246.

Mauseth, J. D. 1993a. Water-storing and cavitation-preventing adaptations in wood of cacti. *Annals of Botany* 72: 81–89.

Mauseth, J. D. 1993b. Medullary bundles and the evolution of cacti. *American Journal of Botany* 80: 928–932.

Mauseth, J. D. 1995. Collapsible water-storage cells in cacti. *Bulletin of the Torrey Botanical Club* 122: 145–151.

Mauseth, J. D. 1996. Comparative anatomy of tribes Cereeae and Browningieae (Cactaceae). *Bradleya* 14: 66–81.

Mauseth, J. D., and B. J. Plemons. 1995. Developmentally variable, polymorphic woods in cacti. *American Journal of Botany* 82: 1199–1205.

Mauseth, J. D., and R. G. Ross. 1988. Systematic anatomy of the primitive cereoid cactus, *Leptocereus quadricostatus. Bradleya* 6: 49–64.

Mauseth, J. D., Y. Uozumi, B. J. Plemons, and J. V. Landrum. 1995. Structural and systematic study of an unusual tracheid type in cacti. *Journal of Plant Research* 108: 517–526.

Mauseth, J. D., T. Terrazas, and S. Loza-Cornejo. 1998. Anatomy of relictual members of subfamily Cactoideae, IOS group 1a (Cactaceae). *Bradleya* 16: 31–43.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nobel, P. S. 1991. Tansley Reveiw 32. Achievable productivities of CAM plants: basis for high values compared with C_3 and C_4 plants. *The New Phytologist* 119: 183–205.

Nobel, P. S. 1994. *Remarkable Agaves and Cacti.* Oxford University Press, New York.

Nobel, P. S. 1998. *Los Incomparables Agaves y Cactos.* Editorial Trillas, Mexico City.

Porembski, S. 1996. Functional morphology of *Aztekium ritteri* (Cactaceae). *Botanica Acta* 109: 167–171.

Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539–673.

Rettig, J. H., H. D. Wilson, and J. R. Manhart. 1992. Phylogeny of the Caryophyllales—gene sequence data. *Taxon* 41: 201–209.

Rodman, J. E., M. K. Oliver, R. R. Nakamura, J. U. McClammer, and A. N. Bledsoe. 1984. A taxonomic analysis and revised classification of the Centrospermae. *Systematic Botany* 9: 297–323.

Rose, M.-J., and W. Barthlott. 1994. Coloured pollen in Cactaceae: a mimetic adaptation to hummingbird-pollination? *Botanica Acta* 107: 402–406.

Rowley, G. D. 1976. A *Lophophora* mimic—*Matucana madisoniorum. Excelsa* 6: 93–94.

Russell, C. E., and P. Felker. 1987. The prickly-pears (*Opuntia* spp., Cactaceae): A source of human and animal food in semiarid areas. *Economic Botany* 41: 433–445.

Saveja, M., and J. D. Mauseth. 1991. Leaf-like structure in the photosynthetic, succulent stems of cacti. *Annals of Botany* 68: 405–411.

Speirs, D.C. 1982. The cacti of western Canada (part 3). *National Cactus and Succulent Journal* 37: 53–54.

Stuppy, W. 2002. Seed characters and generic delimitation in subfamily Opuntioideae. *Succulent Plant Research* (in press).

Thorne, R. F. 1973. Floristic relationships between tropical Africa and tropical America. In *Tropical Forest Ecosystems in Africa and South America: a Comparative Review* (B. J. Meggars, E. S. Ayensu, and W. D. Duckworth, eds.). Smithsonian Institute Press, Washington, D.C. Pp. 27–47.

Thorne, R. F. 1983. Proposed new realignments in the angiosperms. *Nordic Journal of Botany* 3: 85–117.

Turner, B. L. 1973. Chemosystematic data: their use in the study of disjunctions. *Annals of the Missouri Botanical Garden* 59: 152–164.

Wallace, R. S. 1995. Molecular systematic study of the Cactaceae: using chloroplast DNA variation to elucidate cactus phylogeny. *Bradleya* 13: 1–12.

Wallace, R. S. 1997. The phylogenetic position of *Mediocactus hahnianus. Cactaceae Consensus Initiatives* 4: 11–12.

Wallace, R. S. 2002. Evidence for the recognition of a fourth subfamily of Cactaceae: Maihuenioideae. *Plant Systematics and Evolution* (in review).

Wallace, R. S., and J. H. Cota. 1996. An intron loss in the chloroplast gene *rpo*C1 supports a monophyletic origin for the subfamily Cactoideae. *Current Genetics* 29: 275–281.

Wallace, R. S., and E. D. Forquer. 1995. Molecular evidence for the systematic placement of *Echinocereus pensilis* (K. Brandegee) J. Purpus (Cactaceae: Cactoideae: Echinocereeae). *Haseltonia* 3: 71–76.

Zappi, D. C. 1994. *Pilosocereus* (Cactaceae). The genus in Brazil. *Succulent Plant Research* 3. David Hunt, Dorset, United Kingdom.

CHAPTER

› 2 ‹

SHOOT ANATOMY AND MORPHOLOGY

Teresa Terrazas Salgado and James D. Mauseth

Introduction
Epidermis and Hypodermis
Fundamental Tissue
- *Chlorenchyma*
- *Inner Cortex*
- *Pith*
- *Mucilage Cells, Laticifers, and Sclereids*
- *Mineral Inclusions*

Vascular Tissue
- *Cortical and Medullary Bundles*
- *Xylem*
- *Phloem*

Wood
Morphology
Biomechanics
Conclusions and Future Prospects
Literature Cited

Introduction

Basic anatomical features of Cactaceae have been studied since the 16th century (Metcalfe and Chalk 1950; Conde 1975). More recently, other features have been observed for cultivated plants, such as variations in cuticle thickness, number of hypodermal cell layers, and hypodermal wall thickness (Nyffeler and Eglii 1997). Boosfeld (1920) was one of the first to emphasize the correlation of internal anatomy with external form, noting that taxa that have very different external forms can also have very different internal structure. Among the modifications accompanying the evolution of cacti from leafy ancestors that employ C_3 photosynthesis to stem-photosynthetic Crassulacean acid metabolism (CAM) succulents (Chapter 1) are stems with an increased stomatal frequency, a palisade cortex, a large internal surface area due to extensive intercellular spaces, cortical and medullary vascular bundles, wood modifications, and atypical pith features. The wood not only contains the water-conducting tissue (vessels in the xylem) but can also function in support and affect the shape of cacti. In turn, the shape helps dictate the biomechanical properties of the shoot.

Epidermis and Hypodermis

The epidermis is the outermost layer of cells through which all exchanges with the environment occur; it also provides important taxonomic characters to help distinguish between closely related genera, e.g., *Encephalocarpus* and *Pelecyphora* (Boke 1959) or species, e.g., *Neoevansia striata* and *N. zopilotensis* (Herrera-Cardenas et al. 2000). A typical cactus stem generally has a uniseriate (one cell layer thick) epidermis with square or rectangular cells in transverse section. Subsequent epidermal cell divisions parallel to the periclinal (external) walls produce a distinctive multiseriate epidermis in some species of certain genera, including *Astrophytum, Eriosyce, Eulychnia,* and *Pachycereus.* In other taxa, epidermal cell divisions lack a definitive orientation parallel to the periclinal walls, occur in various angles, and may have divisions only in patches rather than for all epidermal cells (Mauseth 1996; Nyffeler and Eggli 1997).

Most cactus species possess thin-walled epidermal cells; however, for a few taxa, such as species of *Armatocereus, Cereus, Jasminocereus,* and *Mammillaria,* the periclinal (external) wall is thicker than the internal and radial walls (Mauseth 1996; Loza-Cornejo and Terrazas 2001). The periclinal epidermal cell wall may be flat or convex. Convex projections are recognized in several species of *Ariocarpus, Ferocactus, Lophophora, Opuntia, Peniocereus, Thelocactus,* and *Turbinicarpus.* For other genera, the convex outer surface is caused by a cell that divides repeatedly in different planes to produce a cluster of epidermal cells (Fig. 2.1A). This type of rough epidermis occurs in several members of the Cactoideae, e.g., *Eriosyce* (Nyffeler and Eggli 1997), *Polaskia* (Gibson and Horak 1978), and *Browningia* (Mauseth 1996). Modifications in the hypodermis of *Uebelmannia* (Mauseth 1984a) also lead to a rough epidermis. Convex projections in the form of papillae arising from a single epidermal cell or as a series of cells can affect transpiration by influencing the boundary layer of air adjacent to a stem surface (Fahn 1986; Nobel 1999).

The hydrophobic cuticle that forms on the external wall of epidermal cells (and often on the internal wall) contains cutin, a mixture of fatty acids that polymerize on exposure to oxygen. Typically, the fatty acids are produced in the protoplasm and then migrate through the plasma membrane and the cell wall. The cuticle commonly is smooth, but in some cacti it is rough and thick, as in *Ariocarpus fissuratus* (Fig. 2.1B). Young epidermal cells near the stem apex are covered by a thin cuticle, but older epidermal cells usually have a thick cuticle when compared with typical dicotyledons. Cuticle thickness varies from 1 µm to more than 200 µm in species of Cactoideae (Loza-Cornejo and Terrazas 2001) and from 8 to 58 µm for species of *Opuntia* (Pimienta-Barrios et al. 1993). Variations in cuticular thickness may be related to the water conserving ability of a species, although a relationship between cuticle thickness and water-stress resistance has not been observed for opuntias (Pimienta-Barrios et al. 1993). A thick cuticle may also increase the reflection of radiation, which will reduce stem temperatures (Nobel 1999).

As indicated, a cuticle can occur on the inner side of epidermal cells, as for *Homalocephala texenis* and *Uebelmannia gummosa* (Mauseth 1984a). Also, the cuticle can penetrate deeply into the anticlinal (radial) walls, as for *Armatocereus, Bergerocactus, Echinocereus, Escontria, Myrtillocactus, Nopalea, Oreocereus,* and *Pereskia* (Gibson and Horak 1978; Mauseth 1984a, 1996; Loza-Cornejo and Terrazas 2001). Another way epidermal cells provide extra protection is for the protoplasm to produce long-chain fatty acids, which polymerize into wax. These also migrate to the outer surface of the external wall and are deposited on the existing cuticle. This epicuticular wax layer can be smooth or consist of particles of diverse sizes and shapes, such as aggregated beads, flakes, or threads (Mauseth 1984a) and is responsible for the grayish or bluish color of certain cactus stems (Gibson and Nobel 1986).

The only physical openings in the epidermis for the exchange of gases with the surrounding air are the stomata; the aperture of each stoma is controlled by two guard cells. Frequently, the stomata and guard cells are at the same level as the other epidermal cells, but sometimes they are located at the bottom of a pit or depression (Mauseth 1984a). In some species, the cuticle on mature tissue is greatly thickened and causes an increase in the distance of the stomata from the turbulent air, which makes the stomata appear sunken. When stomata are at the bottom of pits or surrounded by thick cuticle, the resistance to water vapor loss is increased slightly (Nobel 1999). Species of *Maihuenia, Pereskia, Pereskiopsis,* and *Quiabentia* possess stomata mainly in their leaves (or near the areoles; Mauseth 1999a), whereas most Opuntioideae and Cactoideae have stomata mainly in their stem epidermis. A few species of Cactoideae have stomata restricted to certain regions of the stem, as in the valleys between the ribs or on the edges of the tubercles (Gibson and Nobel 1986; Porembski 1996; Loza-Cornejo and Terrazas 1996; Herrera-Cardenas et al. 2001), and stomata are absent in the epidermis of certain cephalium shoots (Mauseth 1989; Mauseth and Kiesling 1997). Genes that control stomatal development for a leaf epidermis are postulated to be active for the stem epidermis of cacti. This displaced developmental activity has

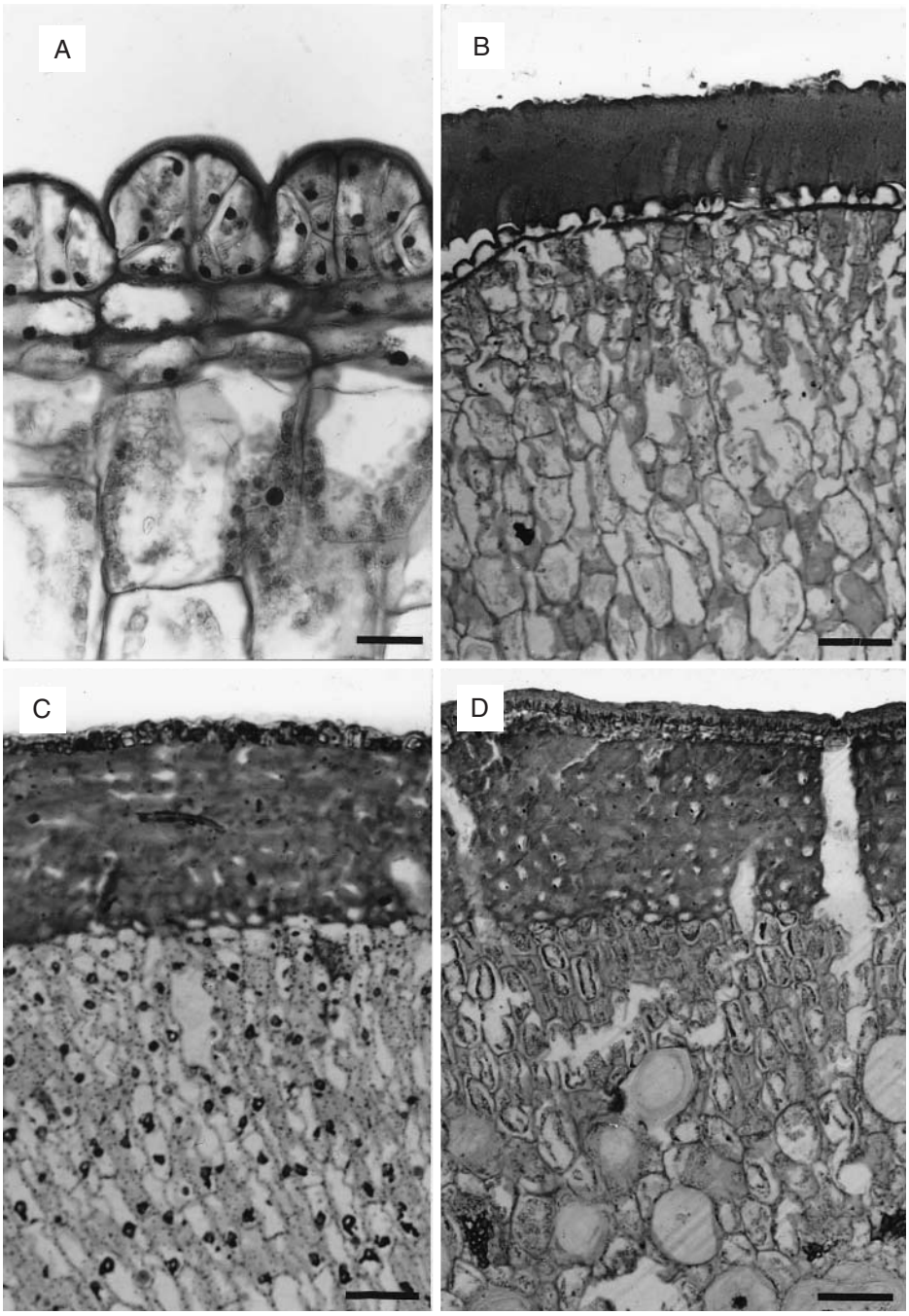


Figure 2.1. Dermal and cortical anatomical characteristics: (A) *Polaskia chende,* epidermal cells with irregular cell divisions and a two layer hypodermis; (B) *Ariocarpus fissuratus,* thick cuticle, papillose epidermal cells and palisade parenchyma cells of the outer cortex; (C) *Cephalocereus columna-trajani,* epidermis with crystals and thick-walled hypodermis; and (D) *Myrtillocactus schenckii,* rough cuticle, thick-walled hypodermis and mucilage cells in the outer cortex. Scale bars: A = 25 µm, B–D = 1 mm.

been called "homeosis" (Sattler 1988; Mauseth 1995a) and may explain other aspects of cactus evolution.

Stomatal frequencies for cacti are low, 20 to 80 per mm^2, compared with leaves of C_3 and C_4 species, where 100 to 300 stomata per mm^2 are common (Nobel 1994, 1999; Nobel and De la Barrera 2000). Within the Cactaceae, stomatal frequencies are highly variable (Table 2.1). Some species of Opuntioideae and Cactoideae have frequencies that are as high as those for the lower leaf epidermis of species of *Pereskia.* The stomatal pore opening for cacti tends to be large compared to other dicotyledons. For instance, for *Opuntia amyclaea, O. ficus-indica, O. joconostle, O. megacantha, O. robusta,* and *O. streptacantha,* the major axis of the pore varies from 33 to 62 μm (Conde 1975; Pimienta-Barrios et al. 1993), whereas pore major axes are typically around 20 μm for non-cacti (Nobel 1999). The pore length is oriented along the longitudinal axis of the stem in Pereskioideae and Opuntioideae, but exhibits a random orientation in most Cactoideae (Eggli 1984; Butterfass 1987). In any case, the area of the open stomatal pores for cacti tends to be less than for leaves of C_3 and C_4 species, reflecting the water-conserving use of CAM by cacti (Nobel 1994, 1999; Chapter 4).

A hypodermis generally occurs under the epidermis and usually consists of more than one cell layer in the stem succulents of the Cactoideae and the Opuntioideae, but is absent in Pereskioideae (Mauseth and Landrum 1997; Mauseth 1999). The number of layers of the hypodermis and the cell wall thicknesses may be related to the rigidity and xeromorphy of the stems. The cell walls of the hypodermis are often thickened with an accumulation of pectin substances, and no hypodermis is lignified (Gibson and Nobel 1986). For *Cephalocereus columna-trajani* (Fig. 2.1C) and *Myrtillocactus schenckii* (Fig. 2.1D), the hypodermis is thick and consists of multiple layers. For *Opuntia* spp. the hypodermis consists of a single layer of cells, many of which contain solitary druses and a multilayered band of strong collenchymatous cells (Conde 1975; Pimienta-Barrios et al. 1993). Because of the druses and its thickness, the hypodermis can affect the penetration of solar radiation to the underlying chlorenchyma and represents a path through which gases must diffuse (Parkhurst 1986; Darling 1989; Pimienta-Barrios et al. 1993).

Fundamental Tissue

The fundamental tissue, cortex and pith, carries out at least two important functions related to xeric adaptations—photosynthesis and water storage. For nearly all cacti, the cortex is the most prominent region of the fundamental tissue and is comprised of long-lived, thin-walled parenchyma cells; even when the epidermis is replaced by periderm (outer bark), the cortex is retained. In both Opuntioideae and Cactoideae the pith tends to maintain its size with the age of the stem and remains alive, which differs from many other dicotyledonous species. The fundamental tissue also includes specialized cells involved with secretion, such as mucilage cells and laticifers. Also, cells in this tissue can produce the alkaloids, hormones, and other chemicals that contribute to metabolism (Mauseth 1984b; Nobel 1988, 1994).

Chlorenchyma

The outer cortex just below the hypodermis is commonly characterized by multiple layers of cells arranged perpendicular to the stem epidermis and is called a palisade cortex, which is made up of parenchyma cells (Figs. 2.1.A–D). The palisade cortex is green and photosynthetic. The cells are radially elongated—generally two to eight times as long as wide. About 13% of *Pereskia* stem tissue is intercellular air space, which is approximately the same as for the palisade parenchyma of its leaves (Sajeva and Mauseth 1991). In most species of the Cactoideae, a layer of parenchyma with large intercellular air spaces, one or two cells thick, occurs between the hypodermis and the palisade cortex. In most Cactaceae the photosynthetic tissue is in the stem, but in *Pereskia* it occurs in leaf palisade and spongy parenchyma as well as the stem cortex, which is narrow with small isodiametric cells (Sajeva and Mauseth 1991). The formation of the palisade cortex in the stems of cacti is similar to that of the palisade parenchyma in dicotyledonous leaves and may similarly involve the breakdown or tearing of the middle lamella accompanied by nonrandom separation of cells, another process of homeosis (Mauseth 1995a).

Inner Cortex

The inner cortex stores water that can be drawn upon during prolonged drought. The outermost layers of this region contain some chlorophyll and presumably carry out some photosynthesis, but the chlorophyll content is progressively lower and becomes absent for the innermost layers. In the Cactoideae, about 9% of the volume of the inner cortex is intercellular air space (Sajeva and Mauseth 1991), but how easily water moves as liquid or vapor is not known. Indeed, succulents undergo successive cycles of filling and emptying their water-storage tissues. Collapsible cortex, a special type of tissue that has flexible and apparently elastic walls, is found in *Bolivicereus, Borzicactus, Cleistocactus, Espostoa, Gymnocalycium, Haageocereus, Jasminocereus, Loxanthocereus,* and many other taxa (Mauseth 1995b; Mauseth et al. 1998). These walls are thin and

TABLE 2.1
Stomatal frequency for photosynthetic tissue in cacti

Subfamily	Frequency (number per mm^2)
Pereskioideae	leaf, 17–99 (51); stem, 2–20 (11)
Opuntioideae	leaf, 7–16 (12) (*Pereskiopsis* spp.); stem, 9–115 (80) (*Opuntia* spp.)
Cactoideae	18–60 (31)

Data indicate the range, with the mean in parentheses, and are from Mauseth and Sajeva (1991), Pimienta-Barrios et al. (1993), Nobel (1994), Arias (1996), and Nobel and De la Barrera (2000).

unlignified and more flexible than those of the palisade cells, readily allowing for volume changes of the cell. Five to ten layers of such cells can occur in the innermost part of the inner cortex, but not in the pith or medullary rays; such cells occur even in regions of shoot tips that are less than one year old, which have never experienced water stress. When drought occurs and the plant's rate of water intake falls below its rate of water loss, the flexible walls permit the collapsible parenchyma cells to release water while the less flexible walls of the palisade cortex cells retain water (Goldstein et al. 1991). Consequently, water from the collapsible water-storage tissue replaces water lost from the photosynthetic tissue.

Most of the water in the stems of cacti is in the inner cortex. The cells have large vacuoles and can lose four times more water than is lost from the smaller cells of the chlorenchyma (Nobel 1994). For the barrel cactus *Ferocactus acanthodes,* solutes decrease in the inner cortex and pith (either by polymerization or transport out of the cells), lowering the osmotic pressure and thereby favoring the redistribution of water to the chlorenchyma (Barcikowski and Nobel 1984). That is, water diffuses from this storage region into regions of higher osmotic pressure in the chlorenchyma. Similar processes occur for the platyopuntia *Opuntia basilaris,* except that for this species most water storage occurs in the pith (Gibson and Nobel 1986). By maintaining higher water content in the chlorenchyma, nocturnal opening of stomata and net CO_2 uptake are allowed to continue for a longer period than would be the case if all the tissue were to dry at the same rate (Chapter 4).

Pith

One difference of many Cactaceae in relation to other dicotyledons is the presence of a radially thick pith in the center of the stem (Bailey 1962, 1963a,b; Gibson and Horak 1978; Mauseth 1989). This pith occurs within the stele and generally occupies a small fraction of the stem volume (Mauseth 1993a), except for platyopuntias (Nobel 1988). The cells are generally thin walled, isodiametric, and living; they act as a water reservoir, often contain starch grains, and may store a variety of allelochemicals. In large-stemmed Cactoideae, the pith may also contain medullary bundles, which facilitate radial water movement (Mauseth 1993a). The short cylindrical, globose, or disc-shaped cacti of the Cacteae, Echinocereae, and Notocacteae tribes lack medullary bundles in their relatively small piths.

Mucilage Cells, Laticifers, and Sclereids

The stem tissues of cacti often contain large quantities of the complex carbohydrate mucilage, which is hydrophilic and affects water relations (Gibson and Nobel 1986; Goldstein and Nobel 1991; Nobel et al. 1992). Mucilage cells (idioblasts that produce mucilage; Fig. 2.2A), which lack chloroplasts and starch grains, were first described by Lauterbach in 1889 (Mauseth 1980). Lloyd (1919) pointed out that although hydrated intracellular mucilage crowds the protoplast, the cell mucilage can aid in cell growth because it imbibes water. The mucilage content and composition in a mucilage cell vary with time of year and species. For older stems or during extensive drought, the mucilage cells may contain crystals (Fig. 2.2B). Both *Pereskia* and *Maihuenia* have mucilage cells, but they are more abundant in *Maihuenia,* for which the very large mucilage cells often compose over half of the leaf volume (Mauseth 1999). Mucilage cells are also abundant in the Cactoideae and Opuntioideae, generally occurring in the inner cortex and pith. Sometimes mucilage cells can occur just below the hypodermis within the palisade parenchyma, as for *Echinocereus sciurus* (Fig. 2.2A). Mucilage cells vary from about 40 μm to over 1.0 mm in diameter and often resemble cavities in the inner cortex, as for *Stenocereus thurberi* and *S. martinezii* (Gibson 1990; Terrazas and Loza-Cornejo 2002). Other mucilage-containing cavities are present in the pith of several species of *Ariocarpus*

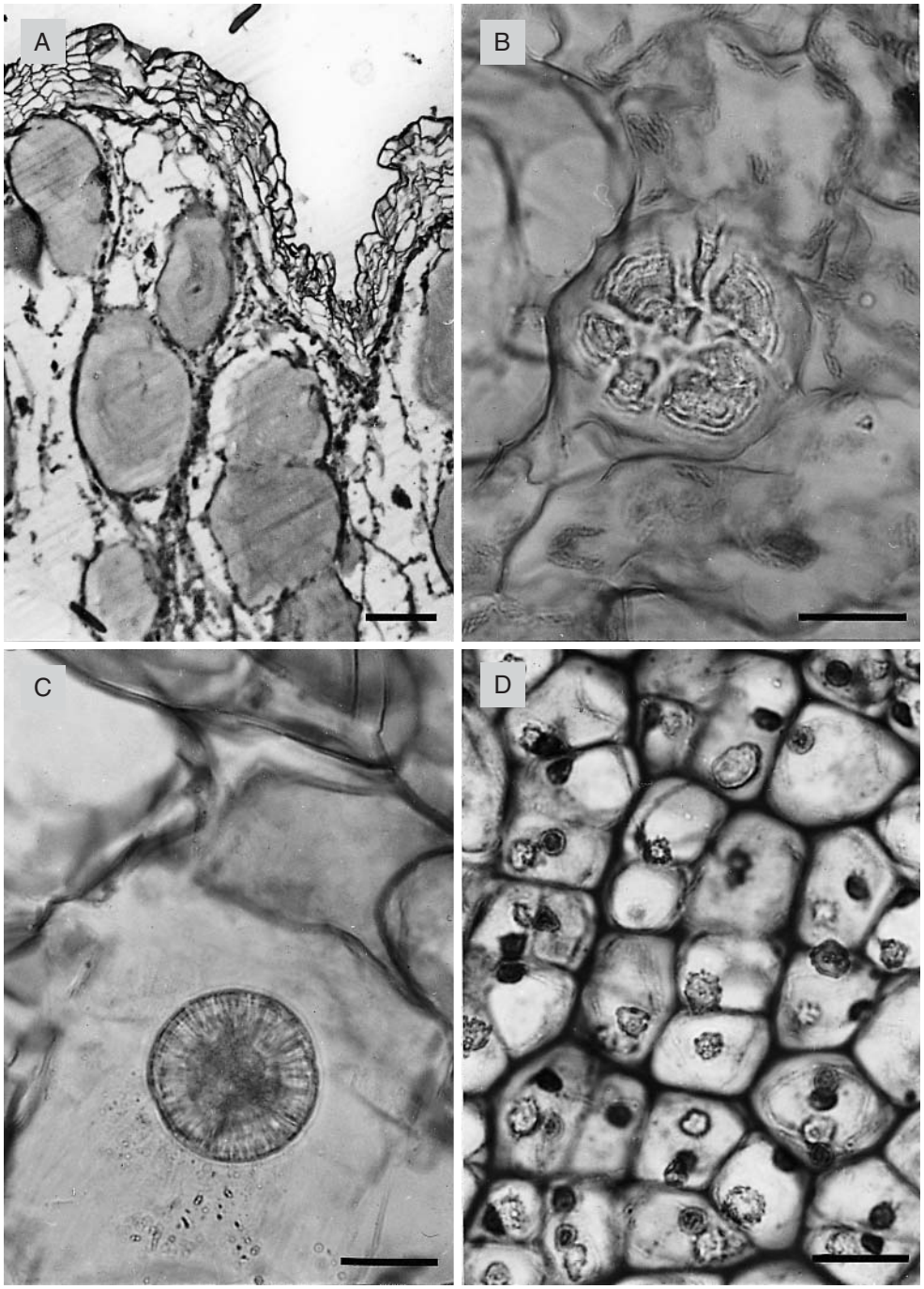


Figure 2.2. Mucilage cells and mineral inclusions: (A) *Echinocereus sciurus,* abundant mucilage cells; (B) *Wilcoxia poselgeri,* crystal in a mucilage cell of the cortical region; (C) *Escontria chiotilla,* sphaerocrystal in the cortical region; and (D) *Stenocereus gummosus,* silica grains in the epidermal cells. Scale bars: A = 1 mm, B = 100 µm, C–D = 20 µm.

(Anderson 1960, 1961), and a unique network of anastomosed canals containing cells essentially filled with mucilage occur in *Nopalea* spp. (Mauseth 1980).

In 1889 Lauterbach reported laticifers (idioblasts that produce latex) for *Coryphantha, Leuchtenbergia,* and *Mammillaria,* but they were not extensively described until 1978 (Mauseth 1978a,b). The composition and abundance of latex varies among species. In the *Mammillaria* section, laticifers are abundant and referred to as "milky," those in section *Subhydrochylus* are referred to as "semi-milky," whereas those in section *Hydrochylus* lack laticifers altogether (Mauseth 1978b). Laticifers in *Mammillaria* differ from those of other plant families and are unique among cacti (Mauseth 1978a). In section *Mammillaria,* laticifers occur in the pith, throughout the cortex, the basal half of the tubercles (modified leaf bases), and even the entire tubercle, where they laterally branch to the hypodermis. Laticifers in section *Subhydrochylus* form only in the outermost cortex and the bases of the tubercles. For plants in sections *Mammillaria* and *Subhydrochylus,* laticifers develop by rapid cell division of wide groups of parenchyma cells. At maturity both have a central lumen lined by an epithelium one to several cell layers thick (Wittler and Mauseth 1984). However, laticifers in section *Subhydrochylus* resemble the ancestral condition because they are more irregular in shape, lumen development, and epithelium form than those in section *Mammillaria.*

Two distinct forms of idioblastic sclereids (dead, lignified cells) occur in the stems of certain columnar cacti, such as *Eulychnia* spp., *Pachycereus pringlei,* and *Stetsonia coryne* (Gibson and Nobel 1986; Nyffeler et al. 1997). One type of sclerenchyma cell is slender and distinctly elongated and occurs in the outer cortex. The other form is globular or subglobular and occurs in the inner cortex and the pith. Sclereids provide mechanical strength due to their thickened, lignified cell walls and aid in lessening collapse of the cortex during drought. Other columnar cacti do not possess idioblastic sclereids, but instead have a cortex with many large mucilage cells, indicating different strategies for adaptation to arid environments.

Mineral Inclusions

Cacti can accumulate enormous quantities of calcium oxalate. For example, up to 85% of the dry weight of *Cephalocereus senilis* can be Ca oxalate (Cheavin 1938). As a result, most cacti have Ca oxalate crystals in their stems, which may be prismatic (sharp angles), druses (star-like), and, rarely, acicular (needles). Crystals are formed in the central vacuole via a complicated precipitation process, which may be an end-product of metabolism and/or may serve as a means of removing excess Ca from the cells (Franceschi and Horner 1980). Plants grown using solutions high in Ca often form more crystals than control plants. In addition to the insoluble Ca salts, many plants contain high concentrations of soluble oxalate, which can affect osmotic pressure (and thus turgor and volume regulation) in the cells. A major function attributed to Ca oxalate crystals is that of protection against foraging animals. The irritation and burning sensations of the mouth caused by eating crystal-containing plants is well known, and large quantities of oxalate can be fatal.

Different forms of Ca oxalate and other chemicals are involved in crystal formation. Using X-ray diffraction, Rivera (1973) found druses with the monohydrate form of Ca oxalate in *Opuntia imbricata* and the dihydrate form in *Echinocactus horizonthalonius, E. intertextus,* and *Escobaria tuberculosa.* The dihydrate form also occurs in prismatic crystals. Leaves of *Pereskiopsis* contain both Ca oxalate and Ca malate crystals (Bailey 1966). Members of Cactoideae may contain sphaerocrystals (spherical; Fig. 2.2C), the composition of which is unknown, and their form differs from other crystal types (Metcalfe and Chalk 1950; Loza-Cornejo and Terrazas 1996). Some species contain only one crystal type, whereas others may have two or more types, even in adjacent cells (Gibson 1973). Crystals are common in secondary xylem and may be deposited in axial or radial parenchyma (Gibson 1973; Mauseth 1996, 1999; Terrazas and Loza-Cornejo 2001).

The occurrence of crystals in the epidermal cells often has taxonomic value (Chapter 1), but their occurrence in the cortex and pith is more variable and therefore has low taxonomic value. For example, *Cephalocereus* and *Neobuxbaumia* are the only members of tribe Pachycereeae with prismatic crystals in their epidermal cells (Gibson and Horak 1978; Terrazas and Loza-Cornejo 2001). Members of tribe Hylocereeae contain acicular crystals in their epidermal cells (Gibson and Nobel 1986; Mauseth et al. 1998; Loza-Cornejo and Terrazas 2001), while other species have distinctive druses in their hypodermal cells (Pimienta-Barrios et al. 1993; Mauseth 1996; Loza-Cornejo and Terrazas 2001).

Silica bodies are also prominent in the epidermal and hypodermal cells of certain cacti and are valuable taxonomically (Fig. 2.2D). Their occurrence is diagnostic for all members of *Stenocereus* and *Rathbunia* (Gibson and Horak 1978). Silica grains also occur in the epidermal cells of other Cactoideae members (Loza-Cornejo and Terrazas 2001) and in the ray cells of *Pachycereus weberi* (Terrazas and Loza-Cornejo 2002), but they have not been observed in the Pereskioideae or Opuntioideae (Gibson and Nobel 1986).

Vascular Tissue

Vascular tissue, which is involved in movement of substances in plants, is highly specialized in cacti. The main and largest vascular bundles occur in the stele, which lies between the inner cortex and the pith. The two tissue types are the xylem, which serves to move water as well as dissolved nutrients, and the phloem, which distributes photosynthetic products and other organic molecules. Primary xylem and phloem develop during the initial stages of growth, and, periodically, secondary tissues subsequently develop. Vascular tissue also occurs in the cortex (cortical bundles) and the pith (medullary bundles).

Cortical and Medullary Bundles

Cortical bundles, which are absent in Pereskioideae and Opuntioideae, generally occur throughout the cortex but do not extend to the hypodermis in members of the Cactoideae (Mauseth 1995a, 1999a). They occur in all directions and change direction frequently. Cortical bundles are collateral and contain primary and secondary xylem and phloem. Secondary phloem accumulates at a higher rate than secondary xylem, which may or may not increase with stem age (Mauseth and Sajeva 1992). For example, for *Mammillaria parkinsonii* and *Pediocactus simpsonii,* older bundles have much more xylem than younger ones. In some species, cortical bundles contain phloem fibers that differentiate adjacent to the conducting cells of the phloem, such as for species of *Acanthocereus* (Mauseth et al. 1998), *Bergerocactus emoryi* (Terrazas and Loza-Cornejo 2002), and *Selenicereus inermis* (Mauseth and Sajeva 1992). Xylary fibers in cortical bundles are rare but occur in *Pilosocereus mortensenii* (Mauseth and Sajeva 1992).

Cortical bundles appear to be involved in three processes (Mauseth and Sajeva 1992): (1) transporting photosynthate from the outer, chlorophyllous palisade cortex to the stele; (2) transporting sugars to and from storage cells in the inner, nonphotosynthetic cortex; and (3) transporting water throughout the cortex. Phloem in cortical bundles is probably involved in sugar transfer when the cortex acts as a starch storage tissue. Cortical bundles accumulate phloem as they age, indicating the continued production of phloem and presumably greater translocation of sugars, which probably cannot be transported from the outer cortex to the stele rapidly enough by diffusion alone (Nobel 1999). Cortical bundles resemble leaf veins in spacing, structure, presence of narrow conducting cells, and solute distribution. Mauseth and Sajeva (1992) conclude that cortical bundles, whose life span in cacti is long compared to the leaf veins in most dicotyledons, have arisen independently in the Cactaceae.

Medullary bundles, which are similar in size to cortical bundles, are initiated close to the apical meristem, may have secondary xylem and phloem, and occur only in subfamily Cactiodeae (Boke 1954; Bailey 1962; Gibson and Horak 1978; Mauseth and Ross 1988; Mauseth 1993a, 1999). Medullary bundles are closely spaced when initiated near the shoot tip, but as the shoots continue growing, the pith expands and medullary bundles are pushed to a wider spacing, with very low densities in the older trunks (Mauseth 1993a). A few species (e.g., *Brachycereus nesioticus, Jasminocereus thouarsii, Monvillea maritima*) are distinctive because primary phloem fibers differentiate adjacent to the medullary bundle phloem. Xylary fibers in medullary bundles are rare but present in *Jasminocereus thouarsii.* Medullary bundles are interconnected with stele bundles, and, in several cases, they completely transverse the broad primary rays and are interconnected with the cortical bundles. Although medullary bundles appear to be relictually absent in the family, they may have originated during the early stages of the evolution of Cactoideae. In fact, a secondary loss of medullary bundles may have occurred in several species of Cactoideae that have a narrow pith and a relatively broad cortex (tribe Cacteae, some Notocacteae, and some Echinocereae; Boke 1956, 1957; Gibson and Horak 1978; Mauseth 1993a; Loza-Cornejo and Terrazas 1996; Mauseth et al. 1998).

Medullary bundles should permit a cactus to translocate water and starch to and from a broad pith. Because they continue to produce phloem throughout the life of the plant and starch is abundant in many pith sections, transport of carbohydrates is an important role for medullary bundles. Water transport throughout the pith may also be important, but may proceed slowly.

Xylem

The water-conducting conduits of the shoots of cacti are vessels occurring either solitary or in small clusters of 2 to 10 vessels (Gibson 1973, 1978). Vessels are narrow, usually ranging from 10 to 60 µm in diameter, are dead at maturity, and consist of tubes of primary and secondary wall (Nobel 1999). The widest vessels occur in the primitive genus *Pereskia* and the narrowest in species of the epiphytic genus *Rhipsalis* (Gibson and Nobel 1986). The vessel elements have simple perforation plates, a highly derived trait that facilitates fluid movement along a vessel (Nobel 1999). Also present are libriform fibers (phloem-like fibers; Fig. 2.3A) and wide-band tracheids (often referred to as vascular tracheids; Fig. 2.3B). Wide-band tracheids are imperforate, broadly fusiform cells with either helical or annular thickenings; the thickenings project deeply into the

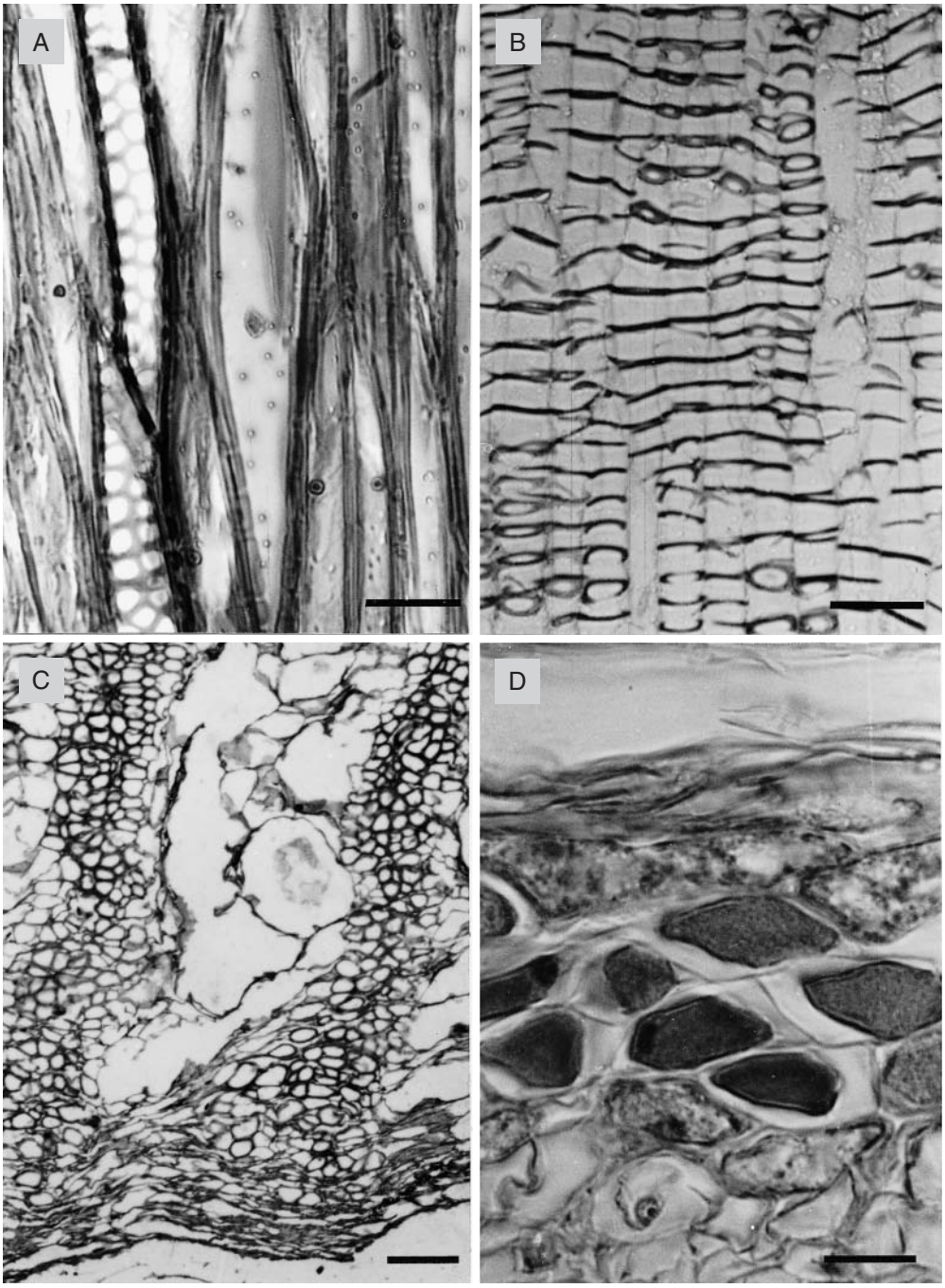


Figure 2.3. Secondary xylem and phloem: (A) *Peniocereus striatus,* distinctive short living fibers; (B) *Echinocereus schmollii,* abundant wide-band tracheids; (C) *Pachycereus pringlei,* sclereid in the collapsed phloem and dilatated rays; and (D) *Wilcoxia poselgeri,* phloem parenchyma cells with tannins between noncollapsed phloem and cortical cells. Scale bars: A, B, D = 20 µm, C = 1 mm.

lumen (Gibson 1973, 1977, 1978; Mauseth et al. 1995; Mauseth and Plemons 1995). Because wide-band tracheids lack perforations, they play little role in rapid water conduction between adjacent cells. Rays in cacti are extremely variable in width and length but are generally wider than in typical dicotyledons, an adaptation that facilitates water storage (Gibson and Nobel 1986). Rays also function in the lateral movement of water, as evidenced by the perforations in the ray cell walls for some cacti (Terrazas 2000). In addition to wide rays, other special features of cactus xylem for water storage are that the fiber cell walls are thin, which increases lumen volume, and that vessels and paratracheal parenchyma constitute a large fraction of the volume of the axial system (Mauseth 1993b).

Phloem

Primary and secondary phloem in Cactaceae varies among species but is generally composed of sieve tube members, companion cells, and axial and radial parenchyma. In most cacti with elongate stems, the young vascular bundles of the stele may have a cap of primary phloem fibers, which are thick-walled, septate, and nucleated. The size of the phloem fiber cap varies among species but does not appear to be an indicator of phylogenetic relatedness (Mauseth 1996). As secondary phloem accumulates, the older, more peripheral phloem collapses and dies, while the younger non-collapsed phloem near vascular cambium consists of living, functioning cells. The older sieve tube members and companion cells collapse into dark-staining masses that may be oriented either tangentially or radially to the stele.

For some species, parenchyma cells may redifferentiate into sclereids (Fig. 2.3C), as for *Pereskia* and some members of the tribes Browningieae, Cereeae, Echinocereeae, and Pachycereeae (Mauseth 1996; Mauseth et al. 1998; Terrazas and Loza-Cornejo 2002). Other species—usually those with short globose shoots—develop neither primary phloem fibers nor sclereids associated with the collapsed phloem (Gibson and Nobel 1986; Loza-Cornejo and Terrazas 1996; Mauseth et al. 1998; Mauseth 1999a). Species of *Wilcoxia* have specialized parenchyma cells that contain abundant tannins (Fig. 2.3D; Loza-Cornejo and Terrazas 1996). The lack of a phloem fiber cap generally is associated with the occurrence of wide-band tracheids in the secondary xylem (Mauseth et al. 1998). Sclereids or fibers do not form associated to phloem in cephalia of *Leptocereus, Melocactus,* and *Neoabbottia* (Mauseth 1989; Mauseth et al. 1998). Phloem rays expand as secondary growth occurs. Phloem rays have living thin-walled parenchyma cells and may contain abundant mucilage cells or druses. They connect with the primary or secondary xylem rays and may contribute to the distribution of photosynthetic products and other organic molecules.

Wood

Various types of wood occur in the Cactaceae (Gibson and Nobel 1986; Mauseth and Plemons 1995; Mauseth and Plemons-Rodriguez 1998; Arnold and Mauseth 1999). They can be classified according to the type of matrix they have (fibrous, parenchymatous, or wide-band tracheids) or according to the uniformity of wood development (monomorphic or polymorphic). The axial portion of fibrous wood, i.e., the portion produced by fusiform initials and whose cells are elongate parallel to the axis of the shoot, consists of vessels embedded in a matrix of living libriform fibers. Typically, the fibers constitute over half of the wood volume, giving it strength, flexibility, and resistance to breaking. Fibrous wood is found in all cacti that are too large to hold themselves up by turgor pressure—all members of *Pereskia,* aborescent Opuntiodeae, *Armatocereus, Pachycereus,* and other large cacti (Gibson 1973; Mauseth 1992; Mauseth and Landrum 1997; Terrazes 2001). Considerable variation occurs in the anatomical details of the fibrous wood. Most species have fibers that lack septae, whereas in other species all or most of the fibers are septate, with a single septum of primary cell wall. Vessels in fibrous wood are generally wider and less frequent than in other types of wood (Table 2.2). The added strength of fibers may allow for larger vessels, thus increasing water movement per vessel because volume flux is dependent on the vessel radius raised to the fourth power (Nobel 1999).

Parenchymatous wood has a matrix of unlignified parenchyma cells with thin primary cell walls. Parenchymatous wood is too soft to provide significant support to the shoot and is found in cacti whose shoots are procumbent, globose, or immersed in the soil. Within the parenchymatous matrix, vessels are smaller in diameter than for vessels in fibrous wood of taller or older plants (Tables 2.2 and 2.3). The vessels are either solitary or occur in clusters, as in fibrous wood, but they have a tendency to form large clusters of up to 100 vessels and thus are more frequent than for the fibrous wood of larger growth forms (Table 2.2 and 2.3). Rays in parenchymatous wood tend to be large and purely parenchymatous and the cells lack secondary walls. Parenchymatous wood tends to be formed in small amounts, with only a few millimeters from pith to vascular cambium. Even though some shoots can have massive amounts of cortex or pith parenchyma, they never have massive amounts of parenchymatous wood. Vessels within parenchymatous wood are in intimate contact

TABLE 2.2
Mean vessel diameter and frequencies for different types of wood present in the Cactaceae

Subfamily	Vessel diameter (μm)	Vessels/mm^2
Pereskioidae		
Fibrous	59	66
Parenchymatous	—	—
Wide-band tracheids	—	—
Opuntioideae		
Fibrous	58	—
Parenchymatous	—	—
Wide-band tracheids	51	—
Cactoideae		
Fibrous	38	168
Parenchymatous	26	554
Wide-band tracheids	27	196

References: Gibson (1973, 1977a,b, 1978) and Mauseth and Plemons-Rodriguez (1998).

TABLE 2.3
Mean values for four wood anatomical features associated with life-form in subfamilies of the Cactaceae

Subfamily	Vessel diameter (μm)	Vessels/mm^2	Vessel element length (mm)	Fiber length (mm)
Pereskioideae				
Tall plants	59	66	—	878
Intermediate height	—	—	—	—
Short, globose	30	689	—	—
Opuntioideae				
Tall plants	75	10	234	704
Intermediate height	56	23	164	543
Short, globose	44	—	140	463
Cactoideae				
Tall plants	44	131	359	878
Intermediate height	33	296	291	683
Short, globose	27	336	182	369

Data are from Gibson (1973, 1977a,b, 1978), Loza-Cornejo and Terrazas (1996), Mauseth and Plemons-Rodriguez (1998), Bobich and Nobel (2001), and Herrera et al. (2001).

with stored water, which can help prevent embolisms (or help refill cavitated ones; Mauseth 1993a).

Wide-band tracheid wood appears to be highly adaptive for plants in extremely xeric habitats. It typically contains vessels, but in some species vessels exist only as a component of earlywood. Such vessels have essentially the same diameter as for vessels in parenchymatous wood for Cactioideae, but are much less frequent (Table 2.2). Cactus wood of any type virtually never has annual growth rings. The most clear-cut examples of growth rings are restricted to wide-band tracheid wood of North American small cacti (*Ferocactus, Echinocactus,* and relatives), but not to the South American ones (*Gymnocalycium, Echinopsis,* and others). In wood that has annual rings, the presence of a vessel-rich earlywood combined with a latewood of such wide-band tracheids makes growth rings visible to the naked eye. In South American taxa with wide-band tracheid wood, vessels and apotracheal parenchyma are mixed in with late-

wood; consequently, earlywood and latewood are difficult to distinguish, and no growth rings can be detected. Such wood of North American taxa also differs from that of South American taxa with respect to rays. Rows of wide-band tracheids occur next to well defined rows of ray parenchyma cells for North American taxa, whereas in South American taxa, a series of parenchyma cells that appears to be a ray will be interrupted by a single wide-band tracheid.

Existing studies on wide-band tracheids are mainly on Cactoideae and *Maihuenia* in the Pereskioideae/Maihuenioideae. In Opuntioideae, wide-band tracheids occur mostly in the rays, and the wood consists of narrow axial masses. Also for the Opuntioideae, wide-band tracheids, which can be found in either parenchymatous or fibrous wood, are usually in the ground tissue next to the protoxylem and occur as both axial and ray cells in the wood, being larger and more numerous in ray cells that are adjacent to the axial regions than they are in the axial regions (Gibson 1973, 1978). In platyopuntias, wide-band tracheids are often arranged in radial files of three or more, and the annularly thickened secondary cell walls of adjacent cells often alternate, giving them an interlocking appearance (Bobich and Nobel 2001).

Several cactus species have dimorphic or trimorphic wood, meaning that when young, they produce one type of wood, but they produce a distinctly different wood type as they mature (Mauseth and Plemons 1995; Mauseth and Plemons-Rodriguez 1998). A common dimorphism is one in which a plant produces wide-band tracheid wood when the plant is young and small enough that turgor pressure will support the shoot. As the plant becomes taller and heavier, a stronger wood is needed, and fibrous wood is produced. When viewing a transverse section of this wood dimorphism, wide-band tracheid wood will occur near the center of the stem and fibrous wood will occur near the vascular cambium. A second, rather common type is one in which vine-like or hemiepiphytic cacti with elongate shoots clamber through the branches of trees, allowing the cactus shoots to rest on the tree's branches. These will often have fibrous wood in the center and parenchymatous wood near the vascular cambium, reflecting the growth of these cacti, which initially have upright self-supporting branches that eventually lean on tree branches for support.

A third example of dimorphic wood involves *Melocactus,* a genus in which adult plants produce a cephalium (a shoot terminus producing flowers and densely covered by spines or trichomes). While growing as a juvenile, nonflowering plant, the shoot makes fibrous wood, but once it becomes old enough to flower, its morphology changes and switches to making parenchymatous wood. Thus, the lower regions of a *Melocactus* has both types of wood, whereas the cephalium has only the adult-phase, parenchymatous wood. The stimulus that triggers the conversion affects the entire plant simultaneously. For other species, the conversion appears to be related to the age of the cambium at each particular area. For example, the basal part of a plant may have converted to the second type of wood, whereas the upper part of the stem is too young, so the stem is producing two types of wood at the same time.

A particularly intriguing aspect of dimorphic wood is that, when wide-band tracheid wood is present, it is always the first type of wood formed. Dimorphic wide-band tracheid-to-fibrous wood has originated several times, with the wide-band tracheid wood being a juvenile feature produced for only a few years. Small cacti with short life spans generally have the greatest fractions of wide-band tracheid wood in their stems when compared with taller, longer-lived forms. In fact, some of the smallest cacti never produce fibrous wood, having either wide-band tracheid wood or parenchymatous wood throughout their lifespan. For species that normally have small adults with wide-band tracheid wood, exceptionally large individuals may produce fibrous wood once they become old. In taxa such as *Epithelantha* or *Frailea,* plants always remain too small, but individuals in taxa such as *Echinopsis, Soehrensia, Ferocactus, Echinocactus,* and *Echinocereus* may actually produce fibrous wood.

Morphology

Fundamentally, the morphology of cacti is like that of other seed plants: the shoot consists of internodes, nodes where leaves are attached (although leaves are little more than leaf primordia in all Cactoideae), and axillary buds (the spine-producing areoles). The bud scales and leaves of axillary buds have become the signature spines of cacti. An axillary bud produces spines as soon as it is initiated by the shoot apical meristem; afterward it may produce a flower and/or a vegetative branch. Cactus stems exhibit short shoot–long shoot architecture. The areoles with their spine-leaves are short shoots, whereas the body of a cactus is a long shoot with highly reduced green leaves (the long-shoot leaves are not reduced in Pereskioideae and Opuntioideae).

Cactus morphology varies from ordinary trees (*Pereskia,* Fig. 2.4A) to large arborescent Opuntioids (*Opuntia,* Fig. 2.4B) and columnar cacti (*Carnegiea,* Fig. 2.4C; *Pachycereus*) to scrambling succulents (*Acanthocereus; Harrisia; Rathbunia,* Fig. 2.4D) to short-columnar and sparsely branched shrubs (*Echinocereus, Haageocereus*) to unbranched globose forms (*Eriosyce; Mammillaria,* Fig. 2.4E)

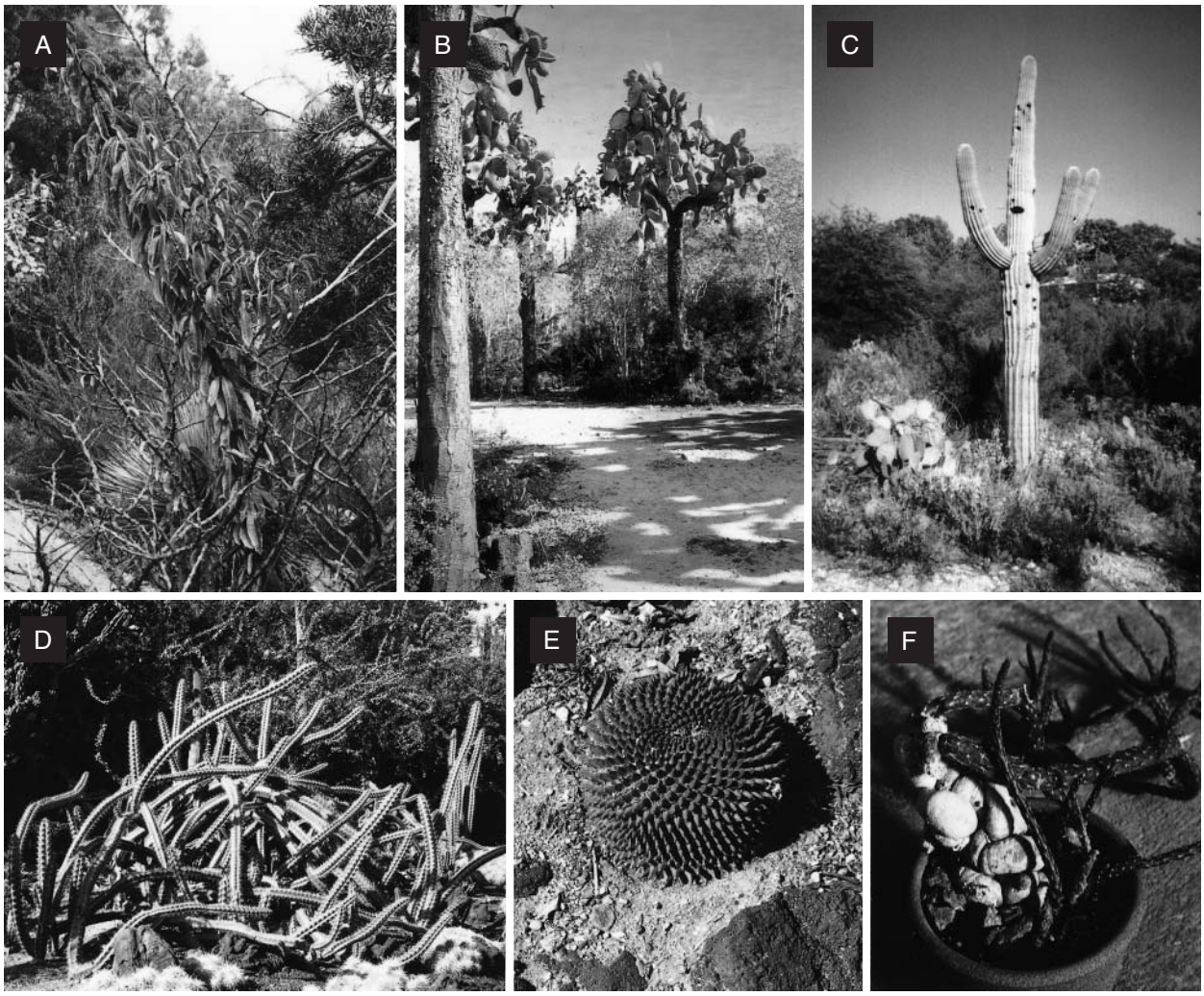


Figure 2.4. Morphology of various cactus species: (A) *Pereskia grandifolia;* (B) *Opuntia echios* var. *gigantea;* (C) *Carnegiea gigantea;* (D) *Rathbunia alamosensis;* (E) *Mammillaria magnimamma;* and (F) *Pterocactus tuberosus.* Photographs are courtesy of Edward G. Bobich (A, C–F) and Park S. Nobel (B).

to geophytes (*Pterocactus,* Fig. 2.4F). Reduction in the number of branches with increased succulence is noteworthy and perhaps is related to the increased weight due to succulence—a cactus with branches as thick as those of a *Pachycereus* or a *Trichocereus* simply cannot have as many branches as does a *Pereskia* in which the branches are slender and relatively light. A correlated change accompanying reduced branching is the reduced number of shoot apical meristems—an unbranched *Cephalocereus, Ferocactus,* or *Soehrensia* has just one single apical meristem with which to construct its entire body. Certainly this has significant consequences. Branching within a taxon is often affected by environmental factors; eg., greater annual precipitation is associated with more infrequent branching in the tribe Pachycereeae (Cornejo and Simpson 1997).

A significant change in morphology with age involves juvenile/adult heteromorphy. For many cacti, mature flowering adults resemble sexually immature plants. However, for genera with cephalia, such as those in *Backebergia* (Fig. 2.5A), *Discocactus,* or *Melocactus* (Fig. 2.5B), older reproductive plants and younger plants do not resemble each other. The juvenile body looks like an ordinary globose cactus with prominent ribs, a green body, widely spaced axillary buds, and larger spines. The cephalium—which is a continuation of the stem, produced by the same apical meristem (Niklas and Mauseth 1981)—lacks ribs, has very closely spaced axillary buds, and produces an abundance of trichomes and short spines that hide the stem surface. The cephalium epidermis converts to cork cambium, so the surface of a cephalium is bark-covered

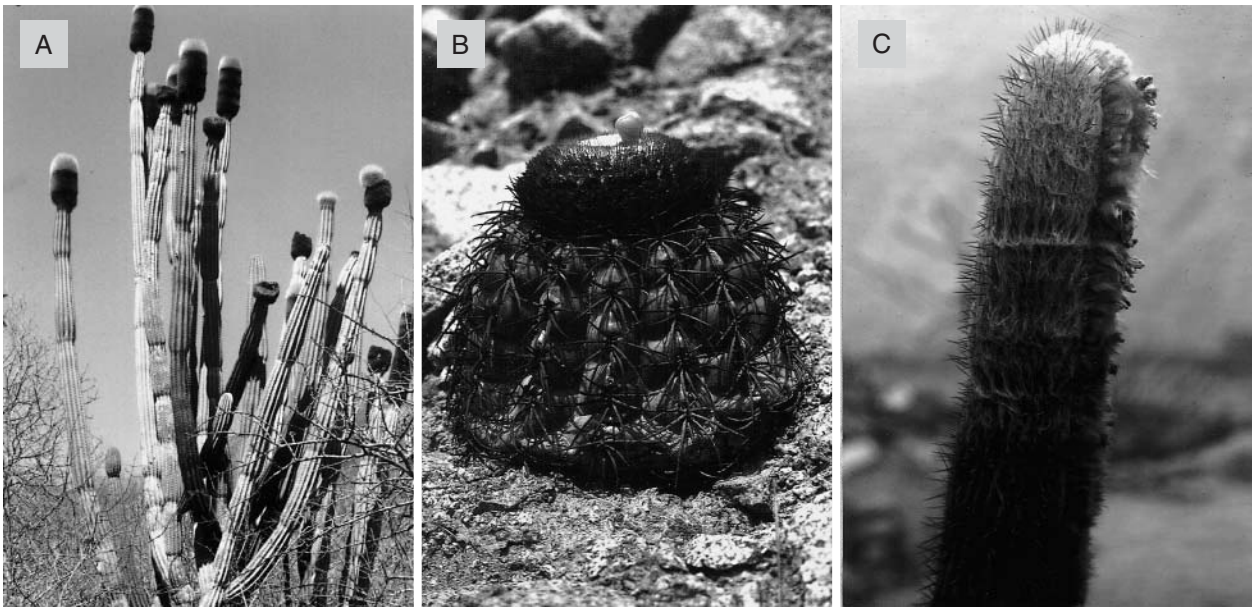


Figure 2.5. Cephalia: (A) apical cephalia for *Backebergia militaris;* (B) apical cephalium for *Melocactus peruvianus;* and (C) lateral cephalium for *Espostoa melanostele.* Photographs are courtesy of Arthur C. Gibson.

and brown (Mauseth 1989). In most cacti, each axillary bud (areole) can produce only a single flower. For cephalia, axillary buds are close together and the stems are narrow, which reduces the expense of producing each new bud (and thus each new flower). Also, because flower production is the only apparent role for cephalia, the buds can be protected with the tight mass of spines and trichomes—a mass so dense that not only are insects prevented from reaching the buds, but so is light (and hence no photosynthesis). Apical cephalia prevent the plant from producing any new photosynthetic tissues, so the photosynthetic capacity decreases with age because the existing photosynthetic tissues become less efficient over time.

Plants with lateral cephalia (Fig. 2.5C) are able to produce both new chlorophyllous tissue and closely spaced, well-protected axillary buds and thus flowers. These plants grow as juveniles for several years; when old enough, several ribs on one side of the body undergo a transition to adult morphology and their axillary buds are able to produce flowers. In addition, they also produce copious trichomes and spines, so the flowers are well protected, and the phyllotaxy of the affected ribs differs from that of the rest of the stem, with buds much closer together. The plants continue to grow like this, with one side being adult, and the other juvenile. Lateral cephalia occur for *Espostoa* (Fig. 2.5C), *Espostoopsis, Micranthocereus, Thrixanthocereus, Vatricania,* and others (Mauseth 1999b). In *Cephalocereus,* the cephalium is initially lateral, but as the plants continue to grow, occasionally adjacent ribs are recruited to the cephalium so the cephalium eventually becomes terminal.

For *Neoraimondia* and *Neocardenasia,* axillary buds can produce several flowers simultaneously and are active year after year (Mauseth and Kiesling 1997). With each flowering, a short shoot stem is produced, but after many years the areoles develop into shoots up to 10 cm long and occasionally even branch. In effect, the short shoots of these genera are a type of cephalium. Members of the genus *Pilosocereus* produce a pseudocephalium. Again, only a few ribs produce flowers as well as copious, long trichomes, but the phyllotaxy is not altered nor is the interior anatomy changed. Once the trichomes break off, the axillary buds that have flowered are more or less indistinguishable from those that never flowered.

Biomechanics

The biomechanics of plant organs are affected by both anatomy and morphology. For all cacti, both wood composition and accumulation affect stem strength (Molina-Freaner et al. 1998; Niklas 2000; Bobich and Nobel 2001). For instance, *Carnegiea gigantea* (saguaro) stems appear to become stiffer over time—possibly due to increases in lignified tissue in the wood—without having appreciable increases in stem diameter, thus allowing plants to become disproportionately slender as height increases (Niklas and Buchman 1994). The amount of lignification of wood,

rather than the fiber length or cell wall thickness, appears to be responsible the for increases in strength with age for the wood of *Pachycereus pringlei* (Niklas et al. 2000). Interestingly, increases in wood strength from the apex to the base for a *P. pringlei* stem is non-linear (Niklas et al. 1999) as a result of the stem wood having less lignin at the base than for regions more than 1 m above the ground (Niklas et al. 2000). This apparently lessens shear stress at the cellular level near the base and also allows for the dissipation of tensile and compressive stresses, thereby decreasing the probability of stem failure at the base. Increases in the frequencies of cells with secondary cell walls, especially libriform fibers, also appears to have a positive correlation with resistance to bending stresses for the junctions between two stem segments (cladodes) for arborescent and frutescent platyopuntias (Bobich and Nobel 2001).

Increases in strength for the junctions of cladodes also correlates with the section modulus of the stem, which increases with wood accumulation (Bobich and Nobel 2001). The same correlation of stem strength with stem diameter is observed in columnar cacti (Molina-Fraener et al. 1998). In fact, slender columnar cacti like *Stenocereus gummosus* may often exceed the critical height allowed by their stem diameter, thus leading to the mechanical failure of the stems. For a threefold increase in length for the cladodes of the arborescent platyopuntia, *Opuntia ficus-indica,* the angular deflection under their own weight approximately doubles, reflecting flexure of both the cladode and the cladode-cladode junction (Nobel and Meyer 1991).

Conclusions and Future Prospects

Because of adaptations to xeric conditions and the presence of less derived woods in Pereskioideae, the Cactaceae is one of the most interesting families both anatomically and morphologically. Increases in water-storage tissue, especially in the cortex and wood, thickened cuticles, and the presence of a hypodermis are all well-known xeromorphic adaptations. However, there is much more to be gained by further anatomical and morphological research. For instance, what causes the presence of wide-band tracheids in wood is relatively unknown. Furthermore, the role of these cells is not fully understood. Also, the "annual growth rings" seen for some cacti need further study; most such anatomical features probably reflect extremely wet versus extremely dry conditions seasonally. A careful study is necessary of the vascular cambium to distinguish between ray and fusiform initials. Finally, the relationship between anatomy and morphology, especially in structural terms, has yet to be investigated for a variety of growth forms, e.g., epiphytes, vine cacti, and shrubby forms. There is indeed much more to be known about the anatomy and morphology that lead to the various forms of cacti.

Acknowledgment

The authors gratefully thank Edward Bobich and Park Nobel for substantial contributions to the writing of this chapter.

Literature Cited

Anderson, E. F. 1960. A revision of *Ariocarpus* (Cactaceae). I. The status of the proposed genus *Roseocactus. American Journal of Botany* 47: 582–589.

Anderson, E. F. 1961. A study of the proposed genus *Roseocactus. Cactus and Succulent Journal* (*U.S.*) 33: 122–127.

Arias, S. 1996. Revisión taxonómica del género *Pereskiopsis* Britton et Rose. Master's Thesis, Universidad Autónoma de México, Mexico City.

Arnold, D. H., and J. D. Mauseth. 1999. Effects of environmental factors on development of wood. *American Journal of Botany* 86: 367–371.

Bailey, I. W. 1962. Comparative anatomy of the leaf-bearing Cactaceae. VI. The xylem of *Pereskia sacharosa* and *Pereskia aculeata. Journal of the Arnold Arboretum* 43: 376–383.

Bailey, I. W. 1963a. Comparative anatomy of the leaf-bearing Cactaceae. VIII. The xylem of pereskias from southern Mexico and Central America. *Journal of the Arnold Arboretum* 44: 211–216.

Bailey, I. W. 1963b. Comparative anatomy of the leaf-bearing Cactaceae. VII. The xylem of pereskias from Peru and Bolivia. *Journal of the Arnold Arboretum* 44: 127–133.

Bailey, I. W. 1966. Comparative anatomy of the leaf-bearing Cactaceae. XVI. The development of water-soluble crystals in dehydrated leaves of *Pereskiopsis. Journal of the Arnold Arboretum* 47: 273–283.

Barcikowski, W., and P. S. Nobel. 1984. Water relations of cacti during desiccation: Distribution of water in tissues. *Botanical Gazette* 145: 110–115.

Bobich, E. G., and P. S. Nobel. 2001. Biomechanics and anatomy of cladode junctions for two *Opuntia* (Cactaceae) species and their hybrid. *American Journal of Botany* 88: 391–400.

Boke, N. H. 1954. Organogenesis of the vegetative shoot in *Pereskia. American Journal of Botany* 41: 619–637.

Boke, N. H. 1956. Developmental anatomy and the validity of the genus *Bartschella. American Journal of Botany* 43: 819–827.

Boke, N. H. 1957. Structure and development of the shoot in *Toumeya. American Journal of Botany* 44: 888–896.

Boke, N. H. 1959. Endomorphic and ectomorphic characters in *Pelecyphora* and *Encephalocarpus. American Journal of Botany* 46: 197–209.

Boosfeld, A. 1920. Beiträge zur vergleichenden Anatomie stammsukkulenter Pflanzen. *Beihungen der Botanisches Centralblatt* 37: 217–258.

Butterfass, Th. 1987. The transverse orientation of stomata. *The Botanical Review* 53: 415–441.

Cheavin, W. H. S. 1938. The crystals and cytoliths found in plant cells. Part. I. Crystals. *Microscope* 2: 155–158.

Conde, L. F. 1975. Anatomical comparisons of five species of *Opuntia* (Cactaceae). *Annals of the Missouri Botanical Garden* 62: 425–473.

Cornejo, D. O., and B. B. Simpson. 1997. Analysis of form and function in North American columnar cacti (tribe Pachycereeae). *American Journal of Botany* 84: 1482–1501.

Darling, M. S. 1989. Epidermis and hypodermis of the saguaro cactus (*Cereus giganteus*): anatomy and spectral properties. *American Journal of Botany* 76: 1698–1706.

Eggli, U. 1984. Stomatal types. *Plant Systematics and Evolution* 146: 197–214.

Fahn, A. 1986. Structural and functional properties of trichomes of xeromorphic leaves. *Annals of Botany* 57: 631–637.

Franceschi, V. R., and H. T. Horner Jr. 1980. Calcium oxalate crystals in plants. *Botanical Review* 46: 361–427.

Gibson, A. C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). *Biotropica* 5: 29–65.

Gibson, A. C. 1977a. Vegetative anatomy of *Maihuenia* (Cactaceae) with some theoretical discussions of ontogenetic changes in xylem cell types. *Bulletin of the Torrey Botanical Club* 104: 35–48.

Gibson, A. C. 1977b. Wood anatomy of opuntias with cylindrical to globular stems. *Botanical Gazette* 138: 334–351.

Gibson, A. C. 1978. Wood anatomy of Platyopuntias. *Aliso* 9: 279–307.

Gibson, A. C. 1990. The systematics and evolution of subtribe Stenocereinae. 8. Organ pipe cactus and its closest relatives. *Cactus and Succulent Journal (U.S.)* 62: 13–24.

Gibson, A. C., and K. E. Horak. 1978. Systematic anatomy and phylogeny of Mexican columnar cacti. *Annals of the Missouri Botanical Garden* 65: 999–1057.

Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer.* Harvard University Press, Cambridge, Massachusetts.

Goldstein, G., and P. S. Nobel. 1991. Changes in osmotic pressure and mucilage during low-temperature acclimation of *Opuntia ficus-indica. Plant Physiology* 97: 954–961.

Goldstein, G., J. L. Andrade, and P. S. Nobel. 1991. Differences in water relations parameters for the chlorenchyma and the parenchyma of *Opuntia ficus-indica* under wet versus dry conditions. *Australian Journal of Plant Physiology* 18: 95–107.

Herrera-Cardenas, R., T. Terrazas, and S. Loza-Cornejo. 2000. Anatomía comparada del tallo y de la raíz de las especies del género *Neoevansia* Marshall (Cactaceae). *Boletín de la Sociedad Botánica de México* 67: 5–16.

Lloyd, F. E. 1919. The origin and nature of the mucilage in the cacti and in certain other plants. *American Journal of Botany* 6: 156–166.

Loza-Cornejo, S., and T. Terrazas. 1996. Anatomía del tallo y de la raíz de dos especies de *Wilcoxia* Britton & Rose (Cactaceae) del noroeste de México. *Boletín de la Sociedad Botánica de México* 59: 13–23.

Loza-Cornejo, S., and T. Terrazas. 2001. Epidermal characteristics of North American Cactoideae. *Journal of Plant Research* (in press).

Mauseth, J. D. 1978a. The structure and development of an unusual type of articulated laticifer in *Mammillaria* (Cactaceae). *American Journal of Botany* 65: 415–420.

Mauseth, J. D. 1978b. Further studies of the unusual type of laticiferous canals in *Mammillaria* (Cactaceae): Structure and development of the semi-milky type. *American Journal of Botany* 65: 1098–1102.

Mauseth, J. D. 1980. Release of whole cells of *Nopalea* (Cactaceae) into secretory canals. *Botanical Gazette* 141: 15–18.

Mauseth, J. D. 1984a. Introduction to cactus anatomy. Part 7. Epidermis. *Cactus and Succulent Journal (U.S.)* 56: 33–37.

Mauseth, J. D. 1984b. Introduction to cactus anatomy. Part 8. Inner body. *Cactus and Succulent Journal (U.S.)* 56: 131–136.

Mauseth, J. D. 1989. Comparative structure-function stud-

ies within a strongly dimorphic plant, *Melocactus intortus* (Cactaceae). *Bradleya* 7: 1–11.

Mauseth, J. D. 1992. Comparative wood anatomy of *Jasminocereus* and *Armatocereus* in Ecuador and the Galapagos Islands. *IAWA Bulletin* 13: 245–246.

Mauseth, J. D. 1993a. Medullary bundles and the evolution of cacti. *American Journal of Botany* 80: 928–932.

Mauseth, J. D. 1993b. Water-storing and cavitation-preventing adaptations in wood of cacti. *Annals of Botany* 72: 81–89.

Mauseth, J. D. 1995a. Ontogenetic mechanisms and the evolution of Cactaceae. *Giornale Botanico Italiano* 129: 429–435.

Mauseth, J. D. 1995b. Collapsible water-storage cells in cacti. *Bulletin of the Torrey Botanical Club* 122: 145–151.

Mauseth, J. D. 1996. Comparative anatomy of tribes Cereeae and Browningieae (Cactaceae). *Bradleya* 14: 66–81.

Mauseth, J. D. 1999a. Anatomical adaptations to xeric conditions in *Maihuenia* (Cactaceae), a relictual, leaf-bearing cactus. *Journal of Plant Research* 112: 307–315.

Mauseth, J. D. 1999b. Comparative anatomy of *Espostoa, Pseudoespostoa, Thrixanthocereus,* and *Vatricania* (Cactaceae). *Bradleya* 17: 33–43.

Mauseth, J. D., and R. G. Ross. 1988. Systematic anatomy of the primitive ceroid cactus *Leptocereus quadricostatus. Bradleya* 6: 49–64.

Mauseth, J. D., and M. Sajeva. 1992. Cortical bundles in the persistent, photosynthetic stems of cacti. *Annals of Botany* 70: 317–324.

Mauseth, J. D., and B. J. Plemons. 1995. Developmentally variable, polymorphic woods in cacti. *American Journal of Botany* 82: 1199–1205.

Mauseth, J.D., and R. Kiesling. 1997. Comparative anatomy of *Neoraimondia roseiflora* and *Neocardenasia herzogiana* (Cactaceae). *Haseltonia* 5: 37–50.

Mauseth, J. D., and J. V. Landrum. 1997. Relictual vegetative anatomical characters in Cactaceae: The genus *Pereskia. Journal of Plant Research* 110: 55–64.

Mauseth, J. D., and B. J. Plemons-Rodriguez. 1998. Evolution of extreme xeromorphic characters in wood: A study of nine evolutionary lines in Cactaceae. *American Journal of Botany* 85: 209–218.

Mauseth, J. D., Y. Uozumi, B. J. Plemons, and J. V. Landrum. 1995. Structural and systematic study of an unusual tracheid type in cacti. *Journal of Plant Research* 108: 517–526.

Mauseth, J. D., T. Terrazas, and L. Loza-Cornejo. 1998. Anatomy of relictual members of subfamily Cactoideae IOS group 1a (Cactaceae). *Bradleya* 16: 41–43.

Metcalfe, C. R., and L. Chalk. 1950. *Anatomy of the Dicotyledons.* Vol. II. Clarendon Press, Oxford.

Molina-Freaner, F., C. Tinoco-Ojanguren, and K. J. Niklas. 1998. Stem biomechanics of three columnar cacti from the Sonoran Desert. *American Journal of Botany* 85: 1082–1090.

Niklas, K. J., and J. D. Mauseth. 1981. Relationships among shoot apical meristem ontogenic features in *Trichocereus pachanoi* and *Melocactus matanzanus* (Cactaceae). *American Journal of Botany* 68: 100–105.

Niklas, K. L., and S. L. Buchman. 1994. The allometry of saguaro height. *American Journal of Botany* 81: 1161–1168.

Niklas, K. L., F. Molina-Freaner, and C. Tinoco-Ojanguren. 1999. Biomechanics of the columnar cactus *Pachycereus pringlei. American Journal of Botany* 86: 688–695.

Niklas, K. L., F. Molina-Freaner, C. Tinoco-Ojanguren, and D. J. Paolillo, Jr. 2000. Wood biomechanics and anatomy of *Pachycereus pringlei. American Journal of Botany* 87: 469–481.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nobel, P. S. 1994. *Remarkable Agaves and Cacti.* Oxford University Press, New York.

Nobel, P. S. 1999. *Physicochemical and Environmental Plant Physiology,* 2nd ed. Academic Press, San Diego, California.

Nobel, P. S., and R. W. Meyers. 1991. Biomechanics of cladodes and cladode-cladode junctions for *Opuntia ficus-indica* (Cactaceae). *American Journal of Botany* 78: 1252–1259.

Nobel, P. S., and E. De la Barrera. 2000. Carbon and water balances for young fruits of platyopuntias. *Physiologia Plantarum* 109: 160–166.

Nobel, P. S., J. Cavelier, and J. L. Andrade. 1992. Mucilage in cacti: Its apoplastic capacitance, associated solutes, and influence on tissue water relations. *Journal of Experimental Botany* 43: 641–648.

Nyffeler, R., and U. Eggli. 1997. Comparative stem anatomy and systematics of *Eriosyce sensu lato* (Cactaceae). *Annals of Botany* 80: 767–786.

Nyffeler, R., U. Eggli, and B. E. Leuenberger. 1997. Noteworthy idioblastic sclereids in the stems of

Eulychnia (Cactaceae). *American Journal of Botany* 84: 1192–1197.

Parkhurst, D. F. 1986. Internal leaf structure: a three-dimensional perspective. In *On the Economy of Plant Form and Function* (T. J. Givinish, ed.). Cambridge University Press, New York. Pp. 215–249.

Pimienta-Barrios, E., M. Loera-Quezada, and L. López-Amezcua. 1993. Estudio anatómico comparativo en colectas del subgénero Opuntia. *Agrociencia serie Fitociencia* 4: 7–21.

Porembski, S. 1996. Functional morphology of *Aztekium ritteri* (Cactaceae). *Botanica Acta* 109: 167–171.

Rivera, E. R. 1973. *Echinocactus intertextus* (Cactaceae): An ultrastructural, physiological and biochemical study. Ph.D. Thesis, University of Texas, Austin.

Sajeva, M., and J. D Mauseth. 1991. Leaf-like structure in the photosynthetic, succulent stems of cacti. *Annals of Botany* 68: 405–411.

Sattler, R. 1988. Homeosis in Plants. *American Journal of Botany* 75: 1606–1617.

Terrazas, T. 2000. Perforated ray cells in genera of Pachycereeae (Cactoideae). *IAWA Journal* 21: 457–462.

Terrazas, T. 2001. Wood anatomy of Pachycereeae (Cactoideae). *IAWA Journal* (submitted).

Terrazas, T., and S. Loza-Cornejo. 2002. Phylogenetic relationships of Pachycereeae: A cladistic analysis based on anatomical-morphological data. In *Evolution, Ecology, and Conservation of the Columnar Cacti and their Mutualists* (T. H. Fleming and A. Valiente-Banuet, eds.). University of Arizona Press, Tucson (in press).

Wittler, G. H., and J. D. Mauseth. 1984. Schizogeny and ultrastructure of developing latex ducts in *Mammillaria guerreronis* (Cactaceae). *American Journal of Botany* 71: 1128–1138.

CHAPTER

› 3 ‹

ROOT STRUCTURE AND FUNCTION

Joseph G. Dubrovsky and Gretchen B. North

Introduction
Structure
Primary Structure
Secondary Structure
Root Types
Development and Growth
Indeterminate Root Growth
Determinate Root Growth
Lateral Root Development
Root System Development
Adaptations to Deserts and Other Arid Environments
Root Distribution in the Soil
Environmental Effects on Root Development
Developmental Adaptations
Water and Mineral Uptake
Root Hydraulic Conductivity
Mineral Uptake
Mycorrhizal and Bacterial Associations
Carbon Relations
Conclusions and Future Prospects
Literature Cited

Introduction

From the first moments of a plant's life cycle, including germination, roots are essential for water uptake, mineral acquisition, and plant anchorage. These functions are especially significant for cacti, because both desert species and epiphytes in the cactus family are faced with limited and variable soil resources, strong winds, and frequently rocky or sandy habitats. The goals of this chapter are to review the literature on the root biology of cacti and to present some recent findings. First, root structure, growth, and development are considered, then structural and developmental adaptations to desiccating environments, such as deserts and tropical tree canopies, are analyzed, and finally the functions of roots as organs of water and mineral uptake are explored.

Structure

Cactus roots are less overtly specialized in structure than are cactus shoots. Even so, root structural properties are fundamental to the ability of cacti to take up water and nutrients quickly, and to endure and recover from drought. An understanding of the relationship between root structure and function is essential to understanding how cacti are able to occupy some of the driest, most nutrient-poor habitats on earth.

Primary Structure

During embryogenesis, an embryonic root, or radicle, is formed. In most cactus species, the radicle is relatively small; for example, for *Echinocactus platyacanthus* the radicle is 320 µm long with a compact root cap of four cell layers covering the tip (Lux et al. 1995). Similarly, a small radicle is a typical feature in *Astrophytum myriostigma, Thelocactus bicolor* (Engelman 1960), and *Stenocereus gummosus* (Dubrovsky 1997b). Meristematic activity at the radicle apex begins approximately 12 hours after the radicle emerges from the seed coat for *S. gummosus* and *Ferocactus peninsulae* var. *townsendianus* (Dubrovsky 1997b). As a result of activity in the root apical meristem, roots grow in length, and the primary root tissues are formed (Esau 1977). The organization of the root apical meristem has been analyzed fully for *Opuntia basilaris* (Freeman 1969) and illustrated for a few other species. The roots of most cacti appear to have a closed apical organization in which each tissue can be traced to initial cells at the apex, as seen for *O. basilaris* (Freeman 1969), *O. arenaria* (Boke 1979), and *E. platyacanthus* (Lux et al. 1995).

Probably the best-studied species with respect to root development and structure is *O. ficus-indica.* The radial pattern of the primary root structure in *O. ficus-indica* does not differ significantly from that of most other dicotyledonous species (North and Nobel 1996). For this species, the external tissue—the epidermis—is composed of compact cells, some of which produce root hairs (Fig. 3.1A). Underlying the epidermis is the cortical tissue complex, which includes the hypodermis (the outermost cortical layer), the cortex proper, and the endodermis (the innermost cortical cell layer). The tissue complex located inward from the endodermis is the vascular cylinder. It comprises a two- or three-cell-layered pericycle and the vascular system, consisting of the xylem, the phloem, and the vascular parenchyma. The root vasculature is polyarch, usually with five to seven xylem poles in cylindropuntias (Hamilton 1970) and with four to eight xylem poles in platyopuntias (Freeman 1969). The pith is composed of parenchyma cells, as seen in *O. basilaris* (Freeman 1969). Occasionally, mucilage cells are found in the primary root (Hamilton 1970).

Differentiation of primary tissues starts soon after cell division stops in the meristem. For *O. basilaris,* the protophloem is first evident at 340 µm from the root cap–root body junction; the protoxylem is first evident at 500 µm and is fully differentiated at 1,400 µm. Casparian strips in the endodermis occur at 500 µm from the junction. The metaxylem begins to develop at the base of the transition zone (region between the root and the hypocotyl) 4 to 5 days after germination and later can be found 1.2 mm from the root apex (Freeman 1969). Primary tissue development is unusually rapid in that as early as 6 days after germination the pericycle cells start to produce the periderm (Freeman 1969), which is the first secondary tissue to develop in platyopuntia roots.

Secondary Structure

For *O. ficus-indica, Ferocactus acanthodes,* and two epiphytic cacti, *Epiphyllum phyllanthus* and *Rhipsalis baccifera,* periderm layers (radially flattened cells just outside the pericycle) are well developed at about 150 to 200 mm from the root tip in young roots. Even young seedlings of cylindropuntias have roots with several corky (suberized) layers (Hamilton 1970). Such layers are more numerous and more heavily suberized closer to the tip of roots that have experienced drought than is the case for roots of well-watered plants (North and Nobel 1992). Back from the root tip, in regions approximately 2 to 4 months old, the cortex external to the periderm dies and is shed (Fig. 3.1B), a process that is also hastened by soil drying. Later in development, the outermost layers of the periderm are also shed as the vascular cylinder enlarges due to secondary growth. For the epiphyte *R. baccifera,* radial fissures open in the outer suberized layers of the periderm as roots swell upon re-watering after drought, thereby enhancing water uptake (North and Nobel 1994).

Within the vascular cylinder of most cactus roots, secondary growth produces wedge-shaped regions of vessels and fibers, separated by rays of parenchyma (Fig. 3.1C). For several species, including platyopuntias such as *O. ficus-indica,* large mucilage cells develop in the parenchyma rays, with a possible consequence for regulating water relations within the vascular cylinder (Preston 1901b; Gibson 1973; North and Nobel 1992; Loza-Cornejo and Terrazas 1996). Other characteristics associated with the parenchyma in the secondary xylem can be the occurrence of calcium oxalate crystals (Fig. 3.1D), the storage of starch, and the development of succulence. With respect to the xylem vessels themselves, secondary growth leads to a nearly

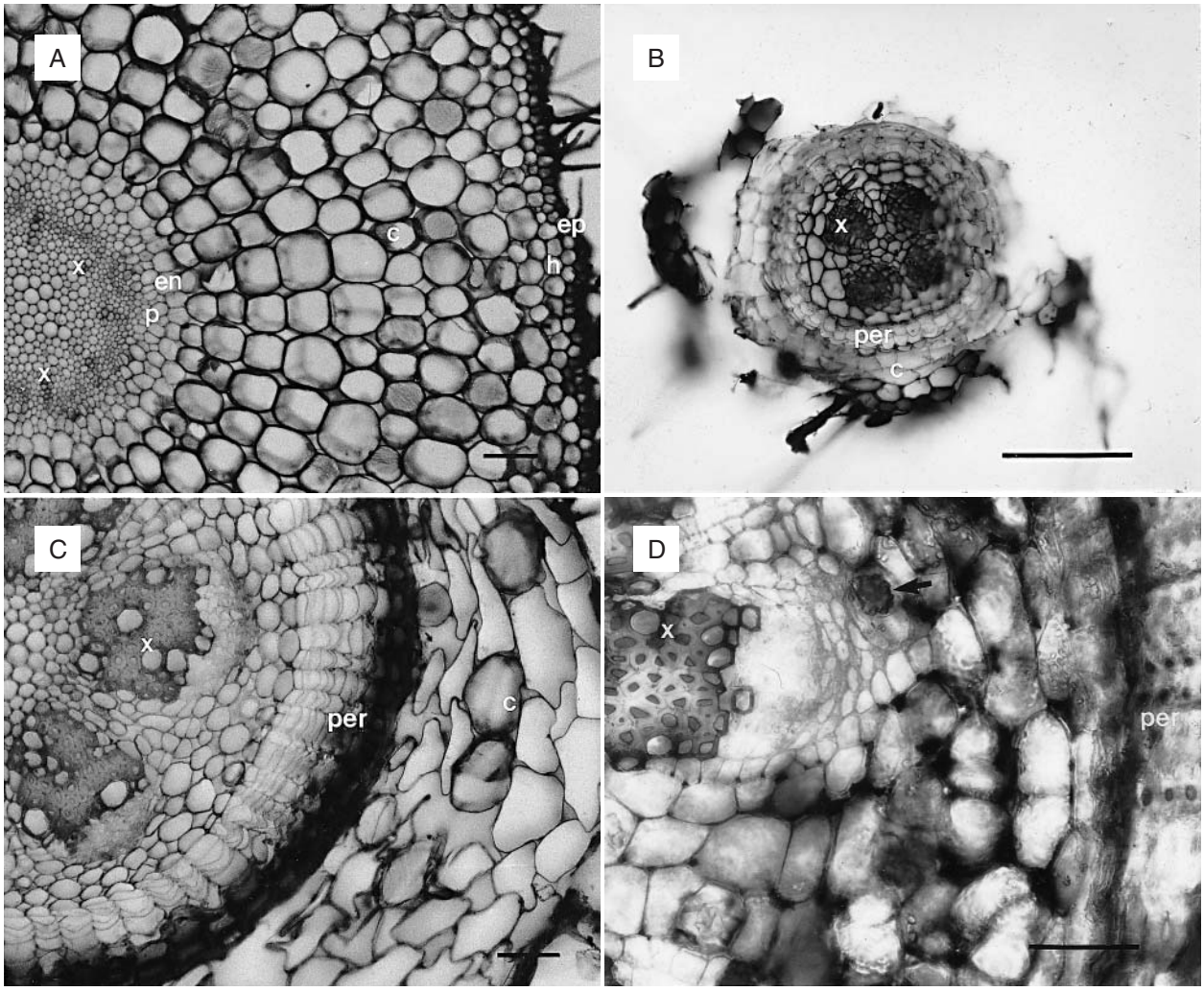


Figure 3.1. Median cross-sections of (A) a 1-month-old root of *Opuntia ficus-indica,* showing primary root tissues; (B) a 3-month-old root of *Epiphyllum phyllanthus,* with cortex separating from the periderm; (C) a 3-month-old root of *O. ficus-indica,* showing secondary growth; and (D) a 5-month-old root of *Rhipsalis baccifera,* with arrow indicating a calcium oxalate crystal. Cell types shown are epidermis (ep), hypodermis (h), cortex (c), endodermis (en), pericycle (p), periderm (per), and xylem (x). Scale bars: A = 50 µm, B = 500 µm, C–D = 100 µm.

threefold increase in mean vessel diameter for *O. ficus-indica* and *F. acanthodes,* and a seven- to tenfold increase in vessel number during 12 months of growth (North and Nobel 1992). For the epiphytes *E. phyllanthus* and *R. baccifera,* mean vessel diameter increases only slightly during 3 months of growth, but vessel number also increases about tenfold (North and Nobel 1994). Such increases in vessel diameter and number are accompanied by large increases in the rate of water transport in the xylem (North and Nobel 1992, 1994).

Root Types

Different types of roots can be classified according to their developmental origin. For example, a root that develops from the embryonic radicle is termed a primary root. Later, when the primary root reaches a certain length, lateral roots are formed. Any root formed on another root is considered a lateral root. When a root is formed on an organ other than a root, it is termed an *adventitious* root. Cladodes of *O. ficus-indica* readily produce adventitious roots at or near areoles (Fabbri et al. 1996; Dubrovsky et al. 1998b), reflecting localized activity in the vascular cambium (Villalobos 1995). For *Pereskia,* adventitious roots can be formed on leaf petioles (Carvalho et al. 1989). Adventitious roots form along the stems of many decumbent, prostrate, and epiphytic cacti, most of which never develop elongated primary roots (Gibson and Nobel 1986). Adventitious rooting of fallen stem segments allows desert

species, such as *O. bigelovii,* to reproduce vegetatively, and the larger water storage capacity of such rooted segments assures greater drought tolerance than is the case for much smaller seedlings. For epiphytic cacti, adventitious rooting along stems can improve anchorage in the canopy, and enables dislodged stem segments to take root where they land on host species (Andrade and Nobel 1997). The ability to produce adventitious roots is also useful for clonal propagation of *O. ficus-indica* and other agronomic species (Le Houérou 1996).

Cactus roots can also be classified according to their function and position within a root system. A century ago, Carleton Preston from Harvard University defined anchoring versus absorbing roots in different cactus species and found some anatomical differences in these root types related primarily to the thickness of the vascular cylinder (Preston 1900, 1901b). William Cannon from the Desert Botanical Laboratory also used these terms, stating that anchoring roots can be: (1) vertically oriented, deeply penetrating, taproots; or (2) horizontally oriented, supporting roots (Cannon 1911). Cannon divided absorbing roots into two categories: (1) rope-like roots and (2) filamentous, relatively thin roots (Cannon 1911). This functional descriptive classification is not absolute, because each root type can have a few functions simultaneously (Preston 1900; Cannon 1911).

Two other root types with morphological modifications are succulent roots and tuberous storage roots, each of which can have some characteristics of the other. Cannon (1911) reported fleshy roots in *O. vivipara,* and first recognized water storage capabilities of the roots of some cactus species. Thick succulent roots (that occasionally include the hypocotyl–root transition zone) can be found in small cacti, such as species of *Ariocarpus* (Britton and Rose 1963; Bravo-Hollis and Sanchez-Mejorada 1978), *Aztekium* (Porembski 1996), *Leuchtenbergia* (Britton and Rose 1963), and *Lophophora* (Nobel 1994). For the columnar cactus *Pachycereus pringlei,* the fleshy taproot can be 18 cm thick near its base (J. G. Dubrovsky, unpublished observations). Succulence develops within the secondary xylem in *Maihuenia patogonica, Nyctocereus serpentinus, Opuntia macrorhiza, O. marenae, Pereskia humboldtii, Pterocactus tuberosus,* and *Tephrocactus russellii,* and in cortical ground tissue in *Neoevansia diguetii* and *Peniocereus greggii* (Gibson 1978). Generally, water storage capacity (capacitance) is relatively small in cactus roots compared to shoots (Nobel 1996). For succulent roots, however, the capacitance is greater than for nonsucculent roots, and may be comparable to that of the water-storage parenchyma in stems. Water-storage tissue in succulent roots has the ability to withstand a high degree of dehydration without irreversible damage, and may also help prevent water loss and decrease root shrinkage during drought.

In addition to storing water, cactus roots frequently accumulate starch. To accommodate starch reserves, the roots of some species acquire a distinct morphology. A relatively large, subterranean storage root is characteristic of cacti that are geophytes; such roots give rise to aboveground annual shoots that shrivel and die during drought and are regenerated the following year, when water is available (Gibson 1978; Gibson and Nobel 1986). Typical geophytes in North America are species of *Neoevansia, O. chaffeyi, Peniocereus,* and *Wilcoxia,* and in South America, *Pterocactus tuberosus* (Gibson 1978). Tuberous roots of *Wilcoxia poselgeri* and *W. tamaulipensis* are characterized by starch-storing parenchyma, primarily in the cortex, along with mucilage cells in the pith, the cortex, and the vascular tissue complex (Loza-Cornejo and Terrazas 1996). Tuberous roots can be sizable; e.g., those of *Peniocereus greggii* grow up to 60 cm in diameter, 15 to 20 cm long, and have a weight of 27 to 56 kg (Britton and Rose 1963). Non-geophytes can also develop one or a few tuberous or tuber-like roots. Groups of tuber-like roots 1 to 2.5 cm in diameter occur for *O. arbuscula* (Cannon 1911), *O. marenae,* and *O. reflexispina* (Felger and Moser 1985). Single tuber-like taproots occur for other non-geophyte species, such as *Ancistrocactus megarhizus* (Britton and Rose 1963), *Escobaria henricksonii* (Glass 1998), *Thelocactus mandragora* (Bravo-Hollis and Sanchez-Mejorada 1978), and *T. subterraneus* (Higgins 1948).

Another specialized root type—aerial roots—are rarely produced by desert cacti. However, aerial roots can occur for *S. gummosus* in the Sonoran Desert (Dubrovsky 1999). This species has decumbent stems that form adventitious roots when branches touch the soil. Aerial roots can develop before such contact, on the lower part of the convex stem or on other portions of the stem (Fig. 3.2). These roots are short, succulent, and sometimes extensively branched, with secondary growth, and can be 3 to 4 mm or more in diameter (Dubrovsky 1999). A possible role for such roots in dew uptake remains to be studied. Under greenhouse conditions, *O. arenaria* is also capable of forming numerous aerial roots (Boke 1979). In epiphytic and climbing species, aerial root development is a common phenomenon, as in plants from the genera *Epiphyllum, Hylocereus,* and *Selenicereus* (Bravo-Hollis and Sánchez-Mejorada 1978).

Root systems can be composed of several different root types and in many combinations. Nevertheless, three basic morphological patterns of root systems are recognized

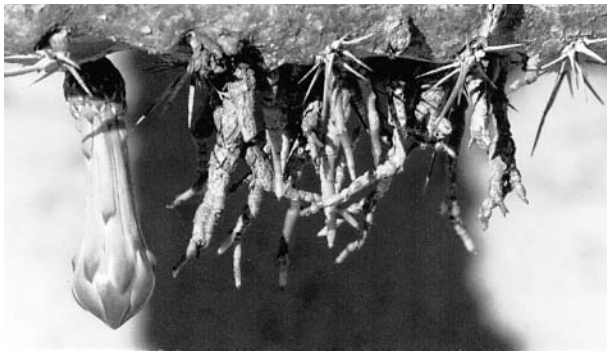


Figure 3.2. Aerial roots on the shoot of *Stenocereus gummosus* in the Sonoran Desert.

(Cannon 1911; Gibson and Nobel 1986). The first type is composed of a taproot with few or no lateral roots, as seen for geophytes and species with succulent roots, such as in the genera *Lobivia* and *Lophophora* (Gibson and Nobel 1986). The second type of root system is composed of a taproot and horizontal, subsurface lateral roots and/or adventitious roots, as occurs for most columnar cacti and species of *Ferocactus* (Cannon 1911; Gibson and Nobel 1986). The third type lacks a taproot and consists of roots of different lengths, with small species tending to have numerous branched roots directly beneath the shoot, and larger species tending to have long subsurface roots extended some length from the shoot, as seen in several species of *Opuntia* (Gibson and Nobel 1986).

Development and Growth

Root development and growth are important, both during the early stages of a plant's life cycle (particularly for seedling establishment) and, later, as continued shoot growth requires that roots invade new areas to obtain water and nutrients. Increases in root surface area are the result of two processes: (1) root elongation, which involves cell production by the root apical meristem; and (2) root branching, or the production of lateral roots. Cells within the root apical meristem can proliferate for an indefinite period, exhibiting indeterminate growth, or they can lose such ability after a limited period, exhibiting determinate growth. The amount and pattern of root branching depends, in part, on whether main roots are characterized by indeterminate or determinate growth.

Indeterminate Root Growth

Indeterminate root growth is common in most flowering plants, including cacti. For example, adventitious roots of *Opuntia ficus-indica* are characterized by indeterminate growth, insofar as cell production by the root apical meristem continues for a relatively long period. The tips of main roots of *O. ficus-indica* generally die after a few months of growth; however, death occurs more quickly in dry soil than in wet soil (Dubrovsky et al. 1998b; G. B. North, unpublished observations). By analyzing the cell lengths along the root, three main root zones can be determined for *O. ficus-indica:* (1) the meristem (where cells are relatively small and are in the cell division cycle), (2) the elongation zone (where cells start and nearly complete rapid elongation), and (3) the differentiation zone (where cells complete their elongation and start to acquire certain tissue characteristics). The root apical meristem of a main adventitious root of *O. ficus-indica* is relatively large—on average 1.1 mm long—consisting of 82 cortical cells in a cell file (Dubrovsky et al. 1998b), comparable to the root meristem of most crop plants. The growing part of the root (the meristem and the elongation zone) in this species is 5 to 7 mm long. The primary root of a Sonoran Desert species, *Pachycereus pringlei,* exhibits indeterminate growth only

TABLE 3.1

Growth characteristics of species with determinate root growth *(Stenocereus gummosus* and *Ferocactus peninsulae)* and indeterminate root growth (*Pachycereus pringlei*) in the first week of the seedling stage

Quantity	*S. gummosus*	*F. peninsulae*	*P. pringlei*
Primary root growth rate (μm hour^{-1})	93 ± 9	111 ± 9	178 ± 7
Length of mature epidermal cells (μm)	98 ± 2	85 ± 3	176 ± 5
Cell number in a file of epidermal cells in the meristem	12.0 ± 0.2	20.9 ± 0.4	20.8 ± 0.4
Duration of the cell division cycle (hours)	9.7 ± 1.1	11.7 ± 0.9	14.5 ± 0.6

The duration of the cell division cycle is estimated by the rate of cell production method (Ivanov and Dubrovsky 1997). Data are means ± SE (n = 11) and are from Dubrovsky et al. (1998a).

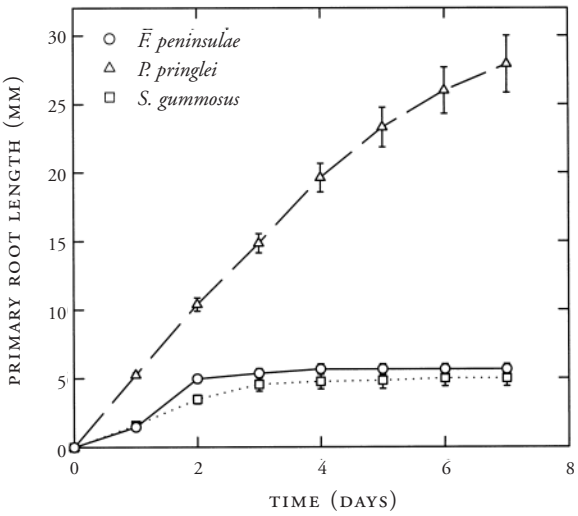


Figure 3.3. Primary root length for *Ferocactus peninsulae, Pachycereus pringlei,* and *Stenocereus gummosus* for 7 days after the start of radicle protrusion. Data are means ± SE (n = 12) and are from Dubrovsky et al. (1998a).

during the first week after germination (Fig. 3.3) and then stops growing. The roots have much shorter meristems, averaging 21 epidermal cells in a cell file (Table 3.1). Smaller root meristems are more typical for young seedlings, because meristem size is correlated with root diameter, and primary and lateral roots are typically thinner than adventitious roots.

The rate of root growth depends on various factors. A primary external factor is temperature, which affects the duration of the cell cycle (cycle time). At an optimal temperature, the average cycle time in the root apical meristem for *O. ficus-indica* is 28 hours (Dubrovsky et al. 1998b) and for *P. pringlei* is 15 hours (Dubrovsky et al. 1998a). A primary internal factor is the final size of elongated cells. The cell length for *O. ficus-indica* averages 378 µm (Dubrovsky et al. 1998b) and for *P. pringlei,* 176 µm (Dubrovsky et al. 1998a). The average cell cycle time within the root apical meristem can vary within and among species, but, in general and assuming elongated cells are the same size, the shorter the cycle, the greater the rate of root growth (Dubrovsky et al. 1998a).

Determinate Root Growth

Determinate root growth is the result of a developmental program in the root apical meristem, in which a finite number of cell division cycles takes place. For cacti, determinate root growth was first described for lateral roots of *Opuntia arenaria* and *O. tunicata* var. *davisii* (Boke 1979). Two types of determinate roots occur for these species. First, relatively long lateral roots (a few cm long) are developed as a part of the absorptive or feeder root system. The apical meristem of these roots has a normal organization, but functions for only a limited time. Soon the root tip dies, and a new meristem is formed behind the dead root tip, giving rise to a sympodially branched system of roots of various lengths. On relatively long roots, short determinate roots of a second type, called "root spurs," develop. The root spur is a cluster of sympodially branched roots less than 1 mm long. The root tip of such spur roots is atypical, lacking a root cap. All cells of the small apical meristem become differentiated, and the tip of the spur root becomes completely covered by root hairs. Spur roots may allow a rapid increase in root surface area, increasing water uptake during infrequent periods of rainfall (Boke 1979).

A determinate pattern of root growth in primary roots is highly unusual for flowering plants. Indeed, continuous elongation of primary roots seems generally more advantageous, particularly for seedling establishment. Surprisingly, determinate root growth is exhibited by the primary root of Sonoran Desert cacti belonging to two tribes, Pachycereeae (*P. pringlei*, *Stenocereus thurberi,* and *S. gummosus;* Dubrovsky 1997a,b) and Cacteae (*Ferocactus peninsulae;* Dubrovsky 1997b). Determinate growth of primary roots is also shown by *S. pruinosus* and *S. standleyi* growing in the Tehuacán Valley of Mexico (Dubrovsky 1999). A similar pattern occurs for epiphytic cacti, including *Epiphyllum phyllanthus,* in which the radicle dies after elongating by only 200 to 400 µm (G. B. North, unpublished observations).

A typical characteristic of cactus roots with determinate growth is the relatively short duration of primary root growth and early meristem exhaustion. For example, *F. peninsulae* and *S. gummosus* grow for only 2 days after the start of radicle protrusion (Fig. 3.3). When seedlings are grown on filter paper, the radicle does not exceed 10 mm, similar to its length in soil (Dubrovsky 1997a,b). When seedlings are grown on sterile medium supplemented with 2% sucrose, the pattern of growth is the same, even though the final size of the roots is greater (Dubrovsky 1997b). During the period of steady-state growth (24–36 hours), meristematic activity is maintained and the size of the root apical meristem remains unchanged. After this period, meristematic cells cease dividing, leave the meristem, and undergo rapid elongation. Because no new cells are produced, the meristem rapidly decreases in size and becomes exhausted. As epidermal cells elongate and differentiate producing hairs, the root hairs grow to the tip of the

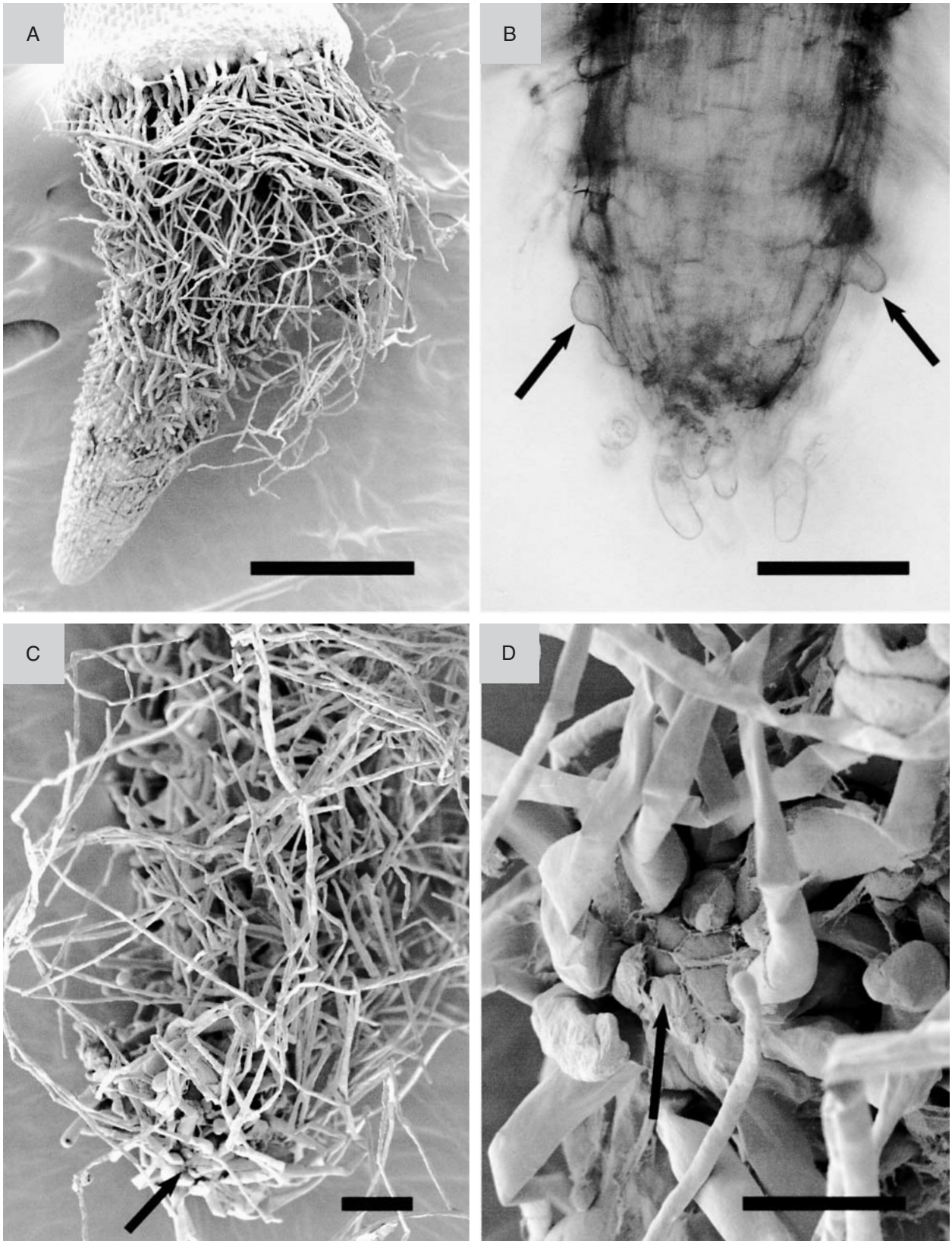


Figure 3.4. Root tips of *Stenocereus gummosus* at (A) 24 hours, (B) 36 hours, and (C) and (D) 48 hours after the start of radicle protrusion. Root hairs (arrows) approach the tip in (A) and (B) and later cover the tip completely in (C). In (D), the five most apical cells (arrow) have not formed root hairs. Scale bars: A = 400 µm, B–C = 100 µm, D = 50 µm.

root and subsequently cover it completely (Fig. 3.4; Dubrovsky 1997b).

The size of the root apical meristem for cacti with determinate root growth is relatively small, with 12 to 21 cells in a cell file (Table 3.1). The cells in the root apical meristem divide relatively quickly, every 10 to 14 hours for *Stenocereus gummosus* and 12 to 17 hours for *Ferocactus peninsulae* (Dubrovsky et al. 1998a). A comparison of the duration of the period of steady-state growth (Dubrovsky 1997a,b) and the duration of the cell division cycle in the root apical meristem (Dubrovsky et al. 1998a) shows that, on average, only two cell division cycles occur in the root apical meristem in both species. Assuming that meristematic activity is maintained until the meristem is exhausted, the maximum number of cycles is four in *S. gummosus* and five in *F. peninsulae.* Thus, the determinate pattern of root growth in these cactus species represents a normal developmental path, during which only a few cell division cycles take place.

Lateral Root Development

For angiosperms, lateral roots originate mainly from the pericycle of a parent root. For *O. basilaris,* the pericycle cells opposite the protoxylem give rise to lateral root primordia early in seedling development (Freeman 1969). For *F. peninsulae* and *S. gummosus,* lateral root primordia can be detected 4 to 5 days after germination (Dubrovsky 1997a,b). The time from primordium initiation to lateral-root emergence is relatively short for these species and comparable to that of other angiosperms (Dubrovsky 1997b). During lateral root development, a vascular junction between the parent root and a lateral root is established, consisting of relatively short tracheary elements with large areas of non-lignified primary cell walls (North et al. 1992), phloem elements, and vascular parenchyma cells. Early in development, lateral root primordia are internal to the periderm, cortex, and epidermis of the parent root (North et al. 1992; North and Nobel 1992). For *Ferocactus acanthodes,* the inner layers of the periderm (the phelloderm layers) of the parent root are continuous with the base of the lateral root, whereas the suberized layers of the periderm (the phellem layers) of the parent root are ruptured as the lateral root elongates (North et al. 1992).

The initiation of lateral root primordia is apparently promoted by drought. For example, the number of second-order lateral root primordia for *F. acanthodes* is significantly greater for plants subjected to drought than for plants under wet conditions (North et al. 1993). In distal root segments of *O. ficus-indica,* four to five more lateral root primordia develop during soil drying than under wet conditions (Dubrovsky et al. 1998b). Similarly, the initiation of lateral root primordia in the epiphytes *E. phyllanthus* and *Rhipsalis baccifera* is stimulated by soil drying (North and Nobel 1994). Because the rate of root growth decreases during drought (Dubrovsky et al. 1998b), the occurrence of primordia closer to the root tip than under wet conditions may reflect reduction in parent root growth, induction of lateral roots, or both. The developmental signals for lateral-root initiation may also include changes in hormone levels due to the death of the parent root tip.

Lateral root elongation after drought is induced by rain or watering, and such lateral roots have been called "rain" roots, although a more general term is "ephemeral roots," because such roots tend to be short-lived (Nobel 1988). Ephemeral roots can emerge rapidly, for example, within 8 hours of watering for both *Opuntia puberula* (Kausch 1965) and *F. acanthodes* (Nobel and Sanderson 1984). Within 24 hours of watering *O. ficus-indica* after 14 days of drought, lateral roots are 2 to 4 mm long, and lateral root growth rate during the second day after emergence is 9.7 mm day^{-1} (Dubrovsky et al. 1998b). Apparently these roots emerge from primordia formed during drought, but further analysis is needed. Ephemeral roots are important for a rapid increase in absorbing surface area without a substantial increase in the distance for water transport (Cannon 1911; Jordan and Nobel 1984; Dubrovsky et al. 1998b). For example, for *F. acanthodes* the total root length increases by 27% because of ephemeral root formation (Jordan and Nobel 1984). During subsequent drought, fine lateral roots can abscise (North et al. 1993), and have thus been called "deciduous roots" (Cannon 1911).

Root System Development

The type and extent of root systems in cacti can vary in response to both external and internal factors. For example, cladodes of *Opuntia versicolor* planted in adobe (clay-containing) soil produce some vertically oriented anchoring roots and some horizontally oriented absorbing roots, whereas cladodes planted in sand produce roots at seemingly random angles (Cannon 1925). The formation of a root system is not necessarily a continuous process in a desert. For example, a seedling may develop roots, then lose them during a subsequent drought, and develop another root system upon re-watering. The duration of drought, the shoot biomass (and thus water storage capacity), and the ability to form sequential root systems all affect seedling survival for *Stenocereus thurberi* (Dubrovsky 1996, 1998, 1999). Most seedlings having fresh weights of 25 to 75 mg lose their root systems completely during a 40-day drought. After rehydration, adventitious roots grow

from the basal portion of the hypocotyl, forming a new root system that is larger than the original one (Dubrovsky 1999). Seedlings and young plants in the desert may develop a number of root systems before forming a lasting, adult root system.

The architecture of a root system is partially determined by whether roots exhibit determinate or indeterminate growth. For plants with determinate primary root growth (e.g., *S. gummosus*), some lateral roots appear to have indeterminate growth. In an adult plant of this species, long rope-like roots can be found, extending 5 to 6 m away from the plant (Dubrovsky 1999). Upon closer inspection, however, such roots are not formed by continuous growth of the root apical meristem, but instead represent a series of interconnected lateral roots (J. G. Dubrovsky, unpublished observations), similar to sympodially branched roots described by Boke (1979).

Adaptations to Deserts and Other Arid Environments

Root Distribution in the Soil

Most desert cacti can be classified as shallow-rooted perennials (Rundel and Nobel 1991). In the Sonoran Desert, the roots of most cacti usually grow no deeper than 15 to 30 cm below the soil surface, although the roots of some species can extend laterally more than 10 m away from the plant base (Cannon 1911). Not surprisingly, the deepest roots are found for columnar cacti. A young plant of *Carnegiea gigantea,* 1.2 m tall, had a stout taproot that penetrated 30 cm and lateral roots that extended 1.5 to 5 m away from the plant, whereas an older, 6.8-m-tall plant had lateral roots up to 9.7 m long that penetrated to a depth of 77 cm (Cannon 1911), perhaps the deepest cactus roots on record.

Root proliferation and elongation is essential for continued water and mineral uptake, and for competition for these resources with other plants. For *Ferocactus acanthodes* at a site in the Sonoran Desert, the dry weight of the whole root system averages only 14% that of the shoot; however, the total surface area of the root system is about 3 times greater than that of the shoot, and the total length of the main roots in the root system per plant averages 182 m (Jordan and Nobel 1984). Roots of *Opuntia polyacantha* growing in the shortgrass steppe of Colorado have a median root depth of less than 2.5 cm (Dougherty et al. 1996). For *O. polyacantha,* as little as 2.5 to 5 mm of precipitation significantly increases cladode biomass. Indeed, the frequency of rain is more important than the absolute amount of rain, due in part to competition with more deeply rooted grasses that capture water from deeper soil levels (Dougherty et al. 1996). In this case, a shallow root distribution not only helps to exploit light rainfall, but also gives the cactus an edge in competition with other plants.

Environmental Effects on Root Development

The root elongation rate depends on temperature. For *F. acanthodes,* root growth in response to temperature can be described by a bell-shaped curve, with maximal elongation at 30°C (Jordan and Nobel 1984). Cactus roots in natural environments are frequently exposed to temperatures higher than optimal; for example, in the northeastern Sonoran Desert, the maximum temperature 5 to 10 cm below the soil surface can be 40 to 50°C (Jordan and Nobel 1984). Cannon (1916) reported that at 43°C, roots cease growing. At 60°C, the root cells of *F. acanthodes* die, although high temperature tolerance of roots in this species can be increased by acclimation. Roots of plants acclimated at day/night temperatures of 45/35°C survive at temperatures 4°C higher than those of plants acclimated at 30/20°C (Jordan and Nobel 1984).

Boulders and subterranean rocks, which are common in desert environments, can provide favorable microsites for cactus root systems. Cannon (1911) observed that rocks stimulated root branching of *Opuntia phaeacantha* var. *discata* in the Sonoran Desert. Similarly, roots of *Echinocereus engelmannii* are more commonly found alongside boulders than at increasing distances away, and lateral roots of *F. acanthodes* are 5.5 times longer and 3 times more numerous under rocks than in regions of the soil without rocks (Nobel et al. 1992b). Such increased growth and branching are explained primarily by a longer period of water availability, as the soil water potential decreases sharply with distance away from rocks and, after soil wetting, remains higher under rocks than in rock-free soil (Nobel et al. 1992b). In addition to creating locally moist microsites, rocks may also be associated with regions of higher nutrient concentrations. During active growth, roots exude carbohydrates to the soil (Huang et al. 1993) and, during subsequent drought, ephemeral roots die. Organic matter may thus accumulate in the vicinity of rocks, promoting new root growth near the rocks when water is again available.

Soil drying generally decreases the rate of root growth, although the rate of drying is critical in determining whether apical elongation can continue. For example, when *Opuntia ficus-indica* is subjected to gradual drying of the substrate, roots have sufficient time for developmental changes to occur, whereas rapid substrate drying leads to death of the apical meristem. The meristem and elongation zone become shorter when the substrate dries gradually,



Figure 3.5. Root system of *Epiphyllum phyllanthus* after 21 days in drying soil, in which all roots are covered by rhizosheaths.

whereas under rapid drying roots die because insufficient time for such rearrangements is available (Dubrovsky et al. 1998b). Similarly, plants of *F. acanthodes* that have been previously exposed to drought suffer less inhibition in root growth under newly imposed water stress than do plants that have not previously been so exposed (Jordan and Nobel 1984).

For a number of desert and epiphytic cacti, soil drying also appears to enhance the development of rhizosheaths, which are rough cylinders around the roots, composed of soil particles that are bound to root hairs and other epidermal cells by mucilage exuded by the roots (Fig. 3.5; Huang et al. 1993; North and Nobel 1992, 1994). Such rhizosheaths become thicker and more cohesive during drought and help improve root water relations, both by ensuring good contact between the root and wet soil and by helping to reduce water loss from the root to a drier soil (North and Nobel 1997).

Developmental Adaptations

Determinate root growth can be viewed as a developmental program well suited to desert conditions. For example, meristem exhaustion in the primary root of *Stenocereus gummosus* coincides with or perhaps triggers the initiation of lateral root primordia. The percentage of roots bearing lateral root primordia is correlated with the percentage of roots in which the root apical meristem is exhausted (Dubrovsky 1997a, 1997b). Determinate primary root growth is thus a developmental mechanism leading to the rapid induction of lateral root formation and root system development. In most desert habitats, the optimum period for seed germination is extremely brief; thus, the rate of root-system formation is a critical factor for successful seedling establishment. Because many of the lateral roots of *S. gummosus* also have determinate growth, a compact root system is formed that requires limited carbon input but is sufficient for water and mineral uptake (Dubrovsky 1997b, 1998).

A related developmental feature with adaptive significance is the relatively short duration of the cell cycle in the root apical meristem for cacti with both determinate and indeterminate root growth. Rapid root elongation and root branching are possible only when new cells are produced rapidly. A relatively short cell cycle can thus be advantageous, particularly during the critical stage of seedling establishment. At a later stage, when established roots resume both apical growth and branching after a drought, a relatively short cell cycle with its high rate of cell production should also enhance the rate of colonization of new soil regions by the roots.

Early root hair production, as seen for *S. gummosus,* represents another developmental adaptation. For this species, root hairs develop almost at the onset of seed germination. When the radicle is still very small, root hairs are evident and are frequently longer than the radicle itself (Fig. 3.4A). The basal epidermal cells, embryonic in origin, average 18 μm in length, whereas the root hairs formed by these cells average 100 times longer (1.8 mm). Each epidermal cell is capable of forming a root hair, unlike the usual case for plants. Later, the epidermal cells that are formed due to root meristem activity average 98 μm in length (Table 3.1). Such early root hair formation, occurring even before germination is completed, can maximize the root surface area available for absorption, thereby increasing water and mineral uptake during the relatively short optimum growth period in a desert (J. G. Dubrovsky, unpublished observations).

Water and Mineral Uptake

Root Hydraulic Conductivity

For both desert and epiphytic cacti, soil moisture varies greatly in both time and space. The success of cacti faced with such heterogeneity in water availability depends on the ability of their roots to conduct water quickly when it is available, to resist water loss when the soil becomes dry, and to resume water uptake upon the cessation of drought. The ability of roots to absorb and transport water is quantified by the root hydraulic conductivity, or L_P. The units of L_P ($m\ s^{-1}\ MPa^{-1}$, where MPa is 10^6 pascals) indicate that a volume of water moves across the root surface area per unit time in response to a difference in pressure (such as the difference between the water potentials of the plant and the soil; Nobel 1999). For roots, L_P has two components, the radial conductivity, which determines the rate of

TABLE 3.2

Hydraulic conductivity (L_P) for young (1-month-old) and older (3- to 5-month-old) roots of two terrestrial cacti (*Ferocactus acanthodes* and *Opuntia ficus-indica*) and two epiphytic cacti (*Epiphyllum phyllanthus* and *Rhipsalis baccifera*) under wet conditions, at 21 to 30 days in drying soil, and at 3 days after soil rewetting

		L_P ($\times 10^{-7}$ m s^{-1} MPa^{-1})		
Species	*Root age*	*Wet soil*	*Drying soil*	*Rewetted soil*
F. acanthodes	young	2.4	1.8	2.0
	older	4.2	1.6	2.6
O. ficus-indica	young	1.7	1.4	1.9
	older	5.4	1.3	1.4
E. phyllanthus	young	2.3	0.7	2.8
	older	5.6	2.6	5.4
R. baccifera	young	2.1	0.7	2.5
	older	7.0	3.2	8.0

Data are from North and Nobel (1992, 1994).

water flow across the root tissues up to the xylem (and which generally is similar in value to L_P), and axial conductivity, which determines the rate of flow through the xylem.

Despite the ability of most cactus roots to endure drought, their L_P under wet soil conditions (Table 3.2) is comparable to that of many mesophytic species, such as *Zea mays* ($1.0–2.8 \times 10^{-7}$ m s^{-1} MPa^{-1}; Steudle et al. 1987) and *Phaseolus vulgaris* ($1.4–4.0 \times 10^{-7}$ m s^{-1} MPa^{-1}; Sands et al. 1982). Three- to 5-month-old roots of both terrestrial and epiphytic cacti have a higher L_P than do 1-month-old roots under wet conditions, due to the higher resistance of the cortex and the immaturity in the xylem of younger roots (North and Nobel 1992, 1994, 1997). During 3 to 4 weeks of soil drying, L_P decreases to about 50% of its value under wet conditions, averaged for young and older roots of the four cactus species (Table 3.2). The decrease is primarily due to reductions in radial conductivity, caused by increased suberization in the periderm, and secondarily to decreases in axial conductivity, due to embolism in the xylem (North and Nobel 1992, 1994, 1996). During the same period of soil drying, root diameter shrinks by 19% for roots of *Opuntia ficus-indica* with rhizosheaths, by 26% for bare roots of this species, and by 13% for older bare roots of *Epiphyllum phyllanthus* (North and Nobel 1992, 1994). Such shrinkage causes air gaps to develop between the root and the soil, which decrease water loss from the root that would otherwise occur due to the higher water potential of the root than of the soil during drought (Nobel and Cui 1992).

In response to soil rewetting after drought, L_P's for roots of both terrestrial and epiphytic cacti increase to equal or exceed their pre-drought values, with the exception of older roots of *Ferocactus acanthodes* and *O. ficus-indica* (Table 3.2). The layers of periderm in these older roots increases in number and in extent of suberization during drought, with a concomitant reduction in their permeability to water (North and Nobel 1992, 1996). Younger root regions lack a periderm, and their permeability is restored by simple rehydration of tissues that, in addition, are protected during drought by the rhizosheaths (North and Nobel 1997). For the younger roots, and for root regions near the junctions between main and lateral roots, numerous lateral root primordia arise during drought and elongate upon rewetting. As these new lateral roots emerge from the parent root, they break through the suberized layers of periderm, thereby increasing root permeability and L_P (North et al. 1993; Dubrovsky et al. 1998b). Once new lateral roots have emerged, the root system for these cacti is capable of rapid water uptake, allowing depleted storage reservoirs to be refilled.

Mineral Uptake

The ability of roots to take up minerals is directly related to their growth. In addition, root growth depends on the nutrient status of the soil. When a mineral resource is in limited supply in the soil, root systems increase in length to explore more area around the plant. As a consequence, relative root biomass (or the root/shoot ratio) tends to be higher in poor soil than in richer soils (Marschner 1986).

Such is the case for cactus plants. In the Sonoran Desert, trees with relatively large canopies (e.g., *Prosopis articulata*) that serve as nurse plants for many cactus species (Nobel 1988) tend to be "islands" rich in nutrients. The concentration of nitrogen (N), phosphorous (P), and carbon (C) in such island soil is 1.4, 1.6, and 1.8 times greater, respectively, than in a treeless region; correspondingly, the root/shoot ratios for plants of *Pachycereus pringlei* grown in island soil are smaller than for plants grown in soil from a treeless region (Carrillo-Garcia et al. 2000).

Mineral uptake by roots can be assessed indirectly from an analysis of the contents of different elements in cactus stem tissues. By abundance, the elements in the stem tissue rank as follows: Ca > K > N > Mg > Na > P > Fe ≥ B > Mn ≥ Zn > Cu > Mo, with the chlorenchyma having higher levels of Ca, Mg, B, and Zn than are found in most agronomic plants (Berry and Nobel 1985). Element concentrations in the cactus stem tissues can be more than 10^3 times greater than in the root substrate, implicating active uptake and transport of ions by the roots (Berry and Nobel 1985; Kolberg and Lajtha 1997). Like cactus stems, roots also accumulate certain elements in their tissues. For example, when boron (B) is applied at a concentration of 15 ppm to soil in which *O. ficus-indica* and *F. acanthodes* are grown, the content of the element in the roots of both species is about 145 ppm. Interestingly, the level of B increases to 2,000 ppm in stem tissues of *O. ficus-indica* and to only 220 ppm in *F. acanthodes* (Berry and Nobel 1985), indicating species differences in element translocation from the root to the shoot. Different species can also vary in their sensitivity to heavy metals. For example, when high concentrations of copper (Cu) and zinc (Zn) are added together to a substrate, the root dry weight of *O. ficus-indica* is reduced more than that of *F. acanthodes* (Berry and Nobel 1985).

Mycorrhizal and Bacterial Associations

Mineral acquisition is frequently related to the activity of fungi and bacteria in the rhizospere. Mycorrhizal associations, important for mineral uptake in many plant species, occur in the root systems of a number of cacti. The characteristic structures indicating infection by vesicular-arbuscular mycorrhizae can be detected in a cleared, longitudinally dissected root of *P. pringlei.* During the first stages of root colonization, the fungus forms an adherent apressorium on the root surface. Subsequently, fungal hyphae penetrate the root, apparently multiplying the internal surface area available for the absorption of limiting mineral nutrients such as P and iron (Fe). In the Sonoran Desert, the level of mycorrhizal colonization ranges from less than 10% of the roots examined in *Mammillaria dioica, P. pringlei, Stenocereus gummosus,* and *S. thurberi,* to 30 to 70% in *F. peninsulae,* to more than 70% in *Cochemia poselgeri, Lophocereus schottii, Opuntia cholla,* and *O. lindsayi* (Carrillo-Garcia et al. 1999). Extensive colonization by three different fungal species in the genus *Glomus* also occurs for roots of *Echinocactus acanthodes, Echinocereus engelmannii, O. acanthocarpa, O. basilaris, O. bigelovii,* and *O. echinocarpa* (Bethlenfalvay et al. 1984). Mycorrhizal associations are found in tropical forest cacti as well, including *Nopalea karwinskiana, O. excelsa,* and *O. puberula* (Allen et al. 1998). For these forest species, mycorrhizal infection increases in proportion to fine root production, which, in turn, is determined by the rainfall pattern (Allen et al. 1998).

Free-living nitrogen-fixing bacteria from the genus *Azospirillum,* present in the rhizosphere of many plant species (Kapulnik 1996), have been isolated from cactus roots as well. For example, *A. lipoferum* occurs in the rhizosphere of species of *Opuntia* growing in India (Rao and Venkateswarlu 1982) and Mexico (Mascarua-Esprarza et al. 1988). Another species, *A. brasilense,* which occurs in the rhizosphere of *O. ficus-indica, S. pruinosus,* and *S. stellatus,* shows nitrogenase activity (ability to fix atmospheric nitrogen) and also exudes the plant hormone auxin, which may induce root branching (Mascarua-Esprarza et al. 1988). When young seedlings of *P. pringlei* are inoculated with *A. brasilense,* the bacteria survives in the plant rhizosphere for up to 300 days (Puente and Bashan 1993). In another experiment, inoculation with *A. brasilense* increases root length but not shoot size, and nitrogenase activity is not detected (Carrillo-Garcia et al. 2000). However, bacteria showing acetylene reduction activity (indicative of nitrogenase activity) are eleven times more abundant in the rhizosphere of ten species of cacti in Mexico than in adjacent bare soil (Loera et al. 1996). A likely role for rhizosheaths in providing conditions favorable to the growth of beneficial bacteria has yet to be explored for cacti.

Carbon Relations

In comparison with most other plants, cacti invest relatively little carbon into the construction and maintenance of roots. This is partly due to the extremely small root/shoot ratio of most succulents (Nobel 1988; Rundel and Nobel 1991), particularly when expressed on a fresh weight basis. It is also due to the relatively low rates of root respiration. Specifically, root respiration, as measured by total CO_2 efflux, is 0.7 and 0.3 mol CO_2 kg^{-1} day^{-1} for young and older roots, respectively, of *Ferocactus acanthodes,* and

1.1 and 0.5 mol CO_2 kg^{-1} day^{-1} for young and older roots of *Opuntia ficus-indica* (Palta and Nobel 1989). Comparable rates for the roots of twelve nondesert angiosperms average 4.8 mol CO_2 kg^{-1} day^{-1} (Lambers 1979). Under drying conditions, root respiration for *F. acanthodes* and *O. ficus-indica* declines even further, averaging 14% of the rate under wet conditions 8 days after water is withheld (Palta and Nobel 1989). The rate of growth respiration, measured as CO_2 given off by newly initiated roots, is also low for cacti in comparison to other plants, averaging about 9 mol CO_2 kg^{-1} day^{-1} for *F. acanthodes* and *O. ficus-indica* (Nobel et al. 1992a), in contrast to 24 mol CO_2 kg^{-1} day^{-1} for nondesert angiosperms (Lambers 1979). Carbon costs are also involved with maintaining mycorrhizal associations and with the creation of rhizosheaths, although young sheathed roots of *O. ficus-indica* exude only about 1% of newly fixed carbon to the soil (Huang et al. 1993).

Conclusions and Future Prospects

Roots and root systems of cacti have evolved structural and physiological features that permit them to withstand environmental stresses, such as high temperatures, prolonged drought, nutrient-poor soils, and strong winds. Developmental adaptations, such as the early formation of root hairs, lateral roots, and periderm, are most significant during the critical period of seedling establishment. The development of rhizosheaths is important for taking up water from moist soil and reducing water loss to dry soil, and the formation of lateral root primordia during drought hastens plant recovery when soil moisture is restored. The shallow distribution of roots in desert and grassland soils helps cacti to exploit limited rainfall, at times in competition with more deeply rooted neighboring plants. Root associations with fungi and bacteria can help in the efficient capture of limited mineral nutrients.

A number of structures and processes in roots of the Cactaceae deserve further investigation. For example, a century ago it was known that roots of *Opuntia arbuscula* are capable of producing shoots (Preston 1901a), and similar "root buds" have been described for *O. arenaria* (Boke 1979). New shoots also appear to arise from the roots of *Myrtillocactus geometrizans* (J. G. Dubrovsky, unpublished observations). Although root buds are a known phenomenon in angiosperms (Peterson 1975), their occurrence in cacti has not been studied. Despite many accounts of ephemeral roots, little is known about root phenology and root plasticity in cacti. The relationship between root growth and shoot activity and how it is affected by environmental variables, such as precipitation, needs to be investigated, particularly in the field. As an example, an understanding of how cactus roots respond to rain occurring in the middle of a summer drought is important for predicting how desert communities will respond to possible climate changes. Studies of mycorrhizal and bacterial associations with cactus roots will also help elucidate phenomena that are less well known for deserts and for tropical canopies than for other plant communities. The nurse-plant association between cacti and other perennial species deserves to be investigated from the perspectives of root competition and root communication, both processes that may also be influenced by fungal and bacterial activity.

In addition to the ecological questions remaining to be addressed for cactus roots, certain basic developmental and physiological processes should be explored for species that can withstand prolonged water stress, such as *Opuntia ficus-indica.* For example, the effects of soil drying on proteinaceous water channels (aquaporins) in the cell membranes of cactus roots can add to the current understanding of such channels in more mesophytic species. The external and internal signals that trigger the initiation of lateral root primordia and other developmental processes, such as determinate root growth and early root hair formation, can be studied in cacti from a wide range of habitats. The role of cactus roots as intermediaries between relatively stable, succulent shoots and heterogeneous, often desiccating soil suggests numerous stimulating possibilities for future research.

Acknowledgment

J.G.B. thanks CONACyT, Mexico (grants 5277-N and 31832-N) for support.

Literature Cited

Allen, E. B., E. Rincón, M. F. Allen, A. Pérez-Jomenez, and P. Huante. 1998. Disturbance and seasonal dynamics of mycorrhizae in a tropical deciduous forest in Mexico. *Biotropica* 30: 261–274.

Andrade, J. L., and P. S. Nobel. 1997. Microhabitats and water relations of epiphytic cacti and ferns in a lowland neotropical forest. *Biotropica* 29: 261–270.

Bethlenfalvay, G. J., S. Dakessian, and R. S. Pacovsky. 1984. Mycorrhizae in a southern California desert: Ecological implications. *Canadian Journal of Botany* 62: 519–524.

Berry, W. L., and P. S. Nobel. 1985. Influence of soil and mineral stresses on cacti. *Journal of Plant Nutrition* 8: 679–696.

Boke, N. H. 1979. Root glochids and root spurs of

Opuntia arenaria (Cactaceae). *American Journal of Botany* 69: 1085–1092.

Bravo-Hollis, H., and H. Sánchez-Mejorada. 1978. *Las Cactáceas de México.* Universidad Nacional Autónoma de México, Mexico City.

Britton, N. L., and J. N. Rose. 1963. *The Cactaceae.* Dover, New York.

Cannon, W. A. 1911. *The Root Habits of Desert Plants.* Publication 131, Carnegie Institution of Washington, Washington, D.C.

Cannon, W. A. 1916. Distribution of the cacti with especial reference to the role played by the root response to soil temperature and soil moisture. *American Naturalist* 50: 435–442.

Cannon, W. A. 1925. *Physiological Features of Roots, with Especial Reference to the Relation of Roots to Aeration of the Soil.* Publication 368, Carnegie Institution of Washington, Washington, D.C.

Carrillo-Garcia, A., J.-L. León de la Luz, Y. Bashan, and G. J. Bethlenfalvay. 1999. Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. *Restoration Ecology* 7: 321–335.

Carrillo-Garcia, A., Y. Bashan, E. Díaz-Rivera, and G. J. Bethlenfalvay. 2000. Effects of resource-island soils, competition, and inoculation with *Azospirillum* on survival and growth of *Pachycereus pringlei,* the giant cactus of the Sonoran Desert. *Restoration Ecology* 8: 65–73.

Carvalho, M.-A. M., W. R. Monteiro, and S. M. C. Dietrich. 1989. Histological aspects of root formation in petioles of detached leaves of *Pereskia grandifolia* (Cactaceae): Natural conditions and effects of GA_3 and dark. *Annals of Botany* 63: 505–514.

Dubrovsky, J. G. 1996. Seed hydration memory in Sonoran Desert cacti and its ecological implication. *American Journal of Botany* 83: 624–632.

Dubrovsky, J. G. 1997a. Determinate primary root growth in *Stenocereus gummosus* (Cactaceae), its organization and role in lateral root development. In *Biology of Root Formation and Development* (A. Altman and Y. Waisel, eds.). Plenum, New York. Pp. 13–20.

Dubrovsky, J. G. 1997b. Determinate primary-root growth in seedlings of Sonoran Desert Cactaceae; its organization, cellular basis, and ecological significance. *Planta* 203: 85–92.

Dubrovsky, J. G. 1998. Determinate root growth as an adaptation to drought in Sonoran Desert Cactaceae. In *Radical Biology: Advances and Perspectives on the Function of Plant Roots* (H. E. Flores, J. P. Lynch, and D. Eissenstat, eds.). American Society of Plant Physiologists, Rockville, Maryland. Pp. 471–474.

Dubrovsky, J. G. 1999. Desarrollo de sistema radicular durante la ontogénesis de plantas del género Stenocereus (Cactaceae). In *El Pitayo en Jalisco y Especies Afines en México* (E. Pimienta-Barrios, ed.). Universidad de Guadalajara, Fundación Produce Jalisco, Guadalajara, Mexico. Pp. 133–146.

Dubrovsky, J. G., L. Contreras-Burciaga, and V. B. Ivanov. 1998a. Cell cycle duration in the root meristem of Sonoran Desert Cactaceae as estimated by cell-flow and rate-of-cell production methods. *Annals of Botany* 81: 619–624.

Dubrovsky, J. G., G. B. North, and P. S. Nobel. 1998b. Root growth, developmental changes in the apex, and hydraulic conductivity for *Opuntia ficus-indica* during drought. *New Phytologist* 138: 75–82.

Dougherty, R. L., W. K. Lauenroth, and J. S. Singh. 1996. Response of a grassland cactus to frequency and size of rainfall events in a North American shortgrass steppe. *Journal of Ecology* 84: 177–183.

Engleman, E. M. 1960. Ovule and seed development in certain cacti. *American Journal of Botany* 47: 460–467.

Esau, K. 1977. *Anatomy of Seed Plants.* Wiley, New York.

Fabbri, A., A. Cicala, and A. Tamburino. 1996. Anatomy of adventitious root formation in *Opuntia ficus-indica* cladodes. *Journal of Horticultural Science* 71: 235–242.

Felger, R. S., and M. B. Moser. 1985. *People of the Desert and Sea. Ethnobotany of the Seri Indians.* University of Arizona Press, Tucson.

Freeman, T. P. 1969. The developmental anatomy of *Opuntia basilaris.* I. Embryo, root, and transition zone. *American Journal of Botany* 56: 1067–1074.

Gibson, A. C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). *Biotropica* 5: 29–65.

Gibson, A. C. 1978. Structure of *Pterocactus tuberosus,* a cactus geophyte. *Cactus and Succulent Journal (U.S.)* 50: 41–43.

Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer.* Harvard University Press, Cambridge, Massachusetts.

Glass, C. E. 1998. *Guide to the Identification of Threatened Cacti of Mexico.* Fidecomiso Fondo para la Biodiversidad, Mexico City.

Hamilton, M. W. 1970. The comparative morphology of three Cylindropuntias. *American Journal of Botany* 57: 1255–1263.

Higgins, V. 1948. Root system of desert plants. *Cactus and Succulent Journal (U.S.)* 20: 71–73.

Huang, B., G. B. North, and P. S. Nobel. 1993. Soil sheaths, photosynthate distribution to roots, and rhizosphere water relations for *Opuntia ficus-indica. International Journal of Plant Sciences* 154: 425–431.

Ivanov, V. B., and J. G. Dubrovsky. 1997. Estimation of the cell-cycle duration in the root meristem: A model of linkage between cell-cycle duration, rate of cell production, and rate of root growth. *International Journal of Plant Sciences* 158: 757–763.

Jordan, P. W., and P. S. Nobel. 1984. Thermal and water relations of roots of desert succulents. *Annals of Botany* 54: 705–717.

Kapulnik, Y. 1996. Plant growth promotion by rhizosphere bacteria. In *Plant Roots: The Hidden Half,* 2nd ed. (Y. Waisel, A. Eshel, and U. Kafkafi, eds.). Marcel Dekker, New York. Pp. 769–781.

Kausch, W. 1965. Beziehungen zwischen Wurzelwachstum, Transpiration und CO_2-Gaswechsel bei einigen Kakteen. *Planta* 66: 229–238.

Kolberg, K., and K. Lajtha. 1997. Population dynamics and trace metal biogeochemistry of the saguaro cactus (*Carnegiea gigantea*) in the Sonoran Desert. *Ecoscience* 4: 223–231.

Lambers, H. 1979. Efficiency of root respiration in relation to growth rate, morphology and soil composition. *Physiologia Plantarum* 56: 18–22.

Le Houérou, H. N. 1996. The role of cacti (*Opuntia* spp.) in erosion control, land reclamation, rehabilitation and agricultural development in the Mediterranean Basin. *Journal of Arid Environments* 33: 135–159.

Loera, T. M. L., J. M. Sánchez-Yañez, and J. J Peña-Cabriales. 1996. Acetylene reduction activity on the root of cactaceous plants. *Revista Latinoamericana de Microbiología* 38: 7–15.

Loza-Cornejo, S., and T. Terrazas. 1996. Anatomía del tallo y de la raíz de dos especies de *Wilcoxia* Britton & Rose (Cactaceae) del Noroeste de México. *Boletín de la Sociedad Botánica de México* 59: 13–23.

Lux, A., Mikuš, M., Hanáčková, Z., and J. Krištín. 1995. Radicle of *Echinocactus platyacanthus* (Cactaceae). *Plant and Soil* 167: 17–21.

Marschner, H. 1986. *Mineral Nutrition of Higher Plants.* Academic Press, London.

Mascarua-Esparza, M. A., R. Villa-Gonzalez, and J. Caballero-Mellado. 1988. Acetylene reduction and indoleacetic acid production by *Azospirillum* isolates from Cactaceous plants. *Plant and Soil* 106: 91–95.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nobel, P. S. 1994. *Remarkable Agaves and Cacti.* Oxford University Press, New York.

Nobel, P. S. 1996. Ecophysiology of roots of desert plants, with special emphases on agaves and cacti. In *Plant Roots: The Hidden Half,* 2nd ed. (Y. Waisel, A. Eshel, and U. Kafrafi, eds.). Marcel Dekker, New York. Pp. 823–844.

Nobel, P. S. 1999. *Physicochemical and Environmental Plant Physiology,* 2nd ed. Academic Press, San Diego, California.

Nobel, P. S., D. M. Alm, and J. Cavelier. 1992a. Growth respiration, maintenance respiration and structural-carbon costs for roots of three desert succulents. *Functional Ecology* 6: 79–85.

Nobel, P. S., and M. Cui, 1992. Shrinkage of attached roots of *Opuntia ficus-indica* in response to lowered water potentials—predicted consequences for water uptake or loss to soil. *Annals of Botany* 70: 485–491.

Nobel, P. S., P. M. Miller, and E. A. Graham. 1992b. Influence of rocks on soil temperature, soil water potential, and rooting patterns for desert succulents. *Oecologia* 92: 90–96.

Nobel, P. S., and J. Sanderson. 1984. Rectifier-like activities of roots of two desert succulents. *Journal of Experimental Botany* 35: 727–737.

North, G. B., F. W. Ewers, and P. S. Nobel. 1992. Main root–lateral root junctions of two desert succulents: Changes in axial and radial components of hydraulic conductivity during drying. *American Journal of Botany* 79: 1039–1050.

North, G. B., and P. S. Nobel. 1992. Drought-induced changes in hydraulic conductivity and structure in roots of *Ferocactus acanthodes* and *Opuntia ficus-indica. New Phytologist* 120: 9–19.

North, G. B., and P. S. Nobel. 1994. Changes in root hydraulic conductivity for two tropical epiphytic cacti as soil moisture varies. *American Journal of Botany* 81: 46–53.

North, G. B., and P. S. Nobel. 1996. Radial hydraulic conductivity of individual root tissues of *Opuntia ficus-indica* (L.) Miller as soil moisture varies. *Annals of Botany* 77: 133–142.

North, G. B., and P. S. Nobel. 1997. Drought-induced

changes in soil contact and hydraulic conductivity for roots of *Opuntia ficus-indica* with and without rhizosheaths. *Plant and Soil* 191: 249–258.

North, G. B., B. Huang, and P. S. Nobel. 1993. Changes in structure and hydraulic conductivity for root junctions of desert succulents as soil water status varies. *Botanica Acta* 106: 126–135.

Palta, J. A., and P. S. Nobel. 1989. Influences of water status, temperature, and root age on daily patterns of root respiration for two cactus species. *Annals of Botany* 63: 651–662.

Porembski, S. 1996. Functional morphology of *Aztekium ritteri* (Cactaceae). *Botanica Acta* 109: 167–171.

Peterson, R. L. 1975. The initiation and development of root buds. In *The Development and Functions of Roots* (J. G.Torrey and D. T. Clarkson, eds.). Academic Press, London. Pp. 125–161.

Preston, C. E. 1900. Observations on the root system of certain Cactaceae. *Botanical Gazette* 30: 348–351.

Preston, C. E. 1901a. Non-sexual propagation of *Opuntia*. *Botanical Gazette* 31: 128.

Preston, C. E. 1901b. Structural studies on southwestern Cactaceae. *Botanical Gazette* 32: 35–55.

Puente, M.-E., and Y. Bashan. 1993. Effect of inoculation with *Azospirillum brasilense* strains on the germination and seedling growth of the giant columnar cardon cactus (*Pachycereus pringlei*). *Symbiosis* 15: 49–60.

Rao, A. V., and B. Venkateswarlu. 1982. Associative symbiosis of *Azospirillum lipoferum* with dicotyledonous succulent plants of the Indian Desert. *Canadian Journal of Microbiology* 28: 778–782.

Rundel, P. W., and P. S. Nobel. 1991. Structure and function in desert root systems. In *Plant Root Growth. An Ecological Perspective* (D. Atkinson, ed.). Blackwell Scientific, London. Pp. 349–378.

Sands, R., E. L. Fiscus, and C. P. P. Reid. 1982. Hydraulic properties of pine and bean roots with varying degrees of suberization, vascular differentiation and mycorrhizal infection. *Australian Journal of Plant Physiology* 9: 559–569.

Steudle, E., R. Oren, and E.-D. Schulze. 1987. Water transport in barley roots. Measurement of hydraulic conductivity, solute permeability, and of reflection coefficients of excised roots using the root pressure probe. *Plant Physiology* 84: 1220–1232.

Villalobos, A. V. M. 1995. Tissue culture application for *Opuntia* sp. pl. micropropagation. In *Agro-Ecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 71–77.

CHAPTER

› 4 ‹

ENVIRONMENTAL BIOLOGY

Park S. Nobel and Edward G. Bobich

Introduction
- *Early Research*
- *Net CO_2 Uptake*
- *Water-Use Efficiency*

Net CO_2 Uptake: Stems
- *Temperature*
- *Water*
- *PPF*
- *Nutrients and Salinity*
- *Atmospheric CO_2*

Net CO_2 Uptake: Fruits

Productivity Responses to Environmental Factors
- *Environmental Productivity Index*
- *Application of EPI to a Barrel Cactus*
- *Application of EPI to a Cultivated Platyopuntia*

Survival
- *Temperature*
- *Water*
- *Salinity*
- *Gravity and Wind*

Conclusions and Future Prospects

Literature Cited

Introduction

Early Research

The Desert Botanical Laboratory of the Carnegie Institution of Washington located just outside Tucson, Arizona, was a major location for early environmental research on cacti, with approximately 100 publications on environmental responses of cacti from its founding in 1903 to its closure in 1940 (McGinnies 1981). The topics studied included root growth, drought tolerance, temperature tolerance, and photosynthesis. Early experiments showed cacti to be limited in growth by low but not by high temperatures, to conserve water, to require much light, and to have special metabolic activity at night.

For instance, root growth of *Opuntia versicolor* was shown to be maximal at 33°C, decreasing 50% at 19°C (Cannon 1925). *Ferocactus wislizenii* could sustain 18 months of drought, during which it lost 70% of its initial

water content, and could survive indoors for 6 years without water (MacDougal et al. 1915). Its osmotic pressure was about 0.4 MPa under wet conditions, increasing to 1.0 MPa after 6 months of drought (MacDougal and Cannon 1910). Maximum tissue acidity was shown to occur in *Carnegiea gigantea* and *Ferocactus acanthodes* in the morning (Long 1915). Indeed, tissue acidity steadily increases about threefold during the night and reversibly decreases during the daytime for *Mammillaria grahamii* and *O. versicolor* (Richards 1915). When the stomates in stems of *C. gigantea* open at night, the stems contract (MacDougal 1924; MacDougal and Working 1933). Stems of *Opuntia phaeacantha* var. *discata* tolerate 1 hour at 62°C (MacDougal and Working 1922). With respect to low temperature, *C. gigantea* tolerates −8°C but not −10°C (Shreve 1931). Cacti also "require all the light that it is possible to give them, the more direct sunshine the better" (Shreve 1931).

In addition to the insights gained from research at the Desert Botanical Garden, other early studies had relevance to the environmental responses of cacti. For instance, cladodes of *Opuntia leucotricha* tend to orient perpendicularly to the direction of a light beam (Goebel 1895). *Opuntia ficus-indica* is injured at −5°C by ice crystals that are initiated extracellularly (Uphof 1916). Moreover, *O. ficus-indica* has a productivity of up to 20 tons dry mass hectare^{-1} year^{-1} (Griffiths 1915). However, the main research on the gas exchange and other environmental responses of cacti did not occur until after World War II, when instruments were developed to measure net CO_2 uptake, transpiration, radiation, temperature, and water potential, using newly invented sensors and electronic circuitry.

Net CO_2 Uptake

Although *O. ficus-indica* has received the most research attention, net CO_2 uptake has been measured for species in all three traditional subfamilies of the Cactaceae (Table 4.1) and for all four subfamilies if Maihuenioideae is separated out of the Pereskioideae. For the Pereskioideae broadly defined, the leaves are the dominant photosynthetic organs, and net CO_2 uptake occurs almost entirely during the daytime using the C_3 photosynthetic pathway. Maximal rates of net CO_2 uptake of 4 to 6 μmol m^{-2} s^{-1} for *Maihuenia poeppigii, Pereskia aculeata,* and *P. grandifolia* occur in the early morning, whereas the stems always have a net CO_2 loss (Nobel and Hartsock 1987). Similar to the Pereskioideae, many of the more primitive species of Opuntioideae have prominent leaves. Maximum net CO_2 uptake rates for leaves of *Austrocylindropuntia subulata, Pereskiopsis porteri,* and *Quiabentia chacoensis* are about 3 μmol m^{-2} s^{-1} during the daytime (Table 4.1). However, in contrast to the case for the stems of species of Pereskioideae, stems of all three leafy species of Opuntioideae had periods of positive net CO_2 uptake, although maximal values averaged only 1 μmol m^{-2} s^{-1} (Nobel 1988).

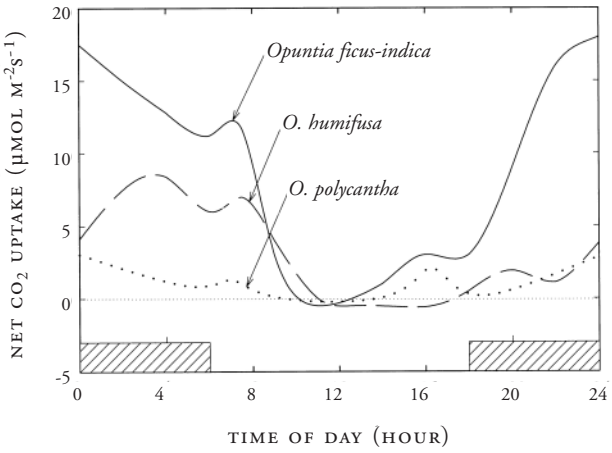


Figure 4.1. Net CO_2 uptake over 24-hour periods for various platyopuntias. Hatched bars indicate nighttime. Data for *Opuntia ficus-indica* are adapted from Cui et al. (1993) and Cui and Nobel (1994), those for *O. humifusa* from Koch and Kennedy (1980), and those for *O. polyacantha* from Gerwick and Williams (1978).

For opuntias, the largest genus in the Opuntioideae, leaves tend to be ephemeral and hence do not contribute substantially to net CO_2 uptake by the entire shoot. Net CO_2 uptake thus occurs primarily by the stems at night (termed Phase I; Osmond 1978) in the Crassulacean acid metabolism (CAM) mode (Fig. 4.1). Some aspects of the gas exchange by an *Opuntia* sp. in Phase I were appreciated by Nicolas Théodore de Saussure in 1804, perhaps the earliest experimental insight into CAM (Richards 1915). The CO_2 taken up is incorporated into an organic acid such as malate using the enzyme phosphoenol pyruvate carboxylase (PEPCase), and the accumulating acids are sequestered into the large vacuoles of chlorenchyma cells (Kluge and Ting 1984). Thus the chlorenchyma becomes progressively more acidic during the night for CAM plants, and its osmotic pressure also increases (Lüttge and Nobel 1984). Under wet conditions and moderate temperatures, some net CO_2 uptake tends to occur in the early morning using 1,5-ribulosebisphosphate carboxylase/oxygenase (Rubisco) via the C_3 pathway before stem and air temperatures have risen appreciably from their minimum nighttime values (Phase II). In fact, carbon isotope evidence indicates that *Opuntia polyacantha* utilizes this phase of the CAM pathway more during wetter, cooler periods around 40,000 years before present (BP) than at 10,000 years BP or at the present time (Troughton et al. 1974).

TABLE 4.1
Summary of maximum rates and total daily net CO_2 uptake for cacti

Subfamily and species	Maximum net CO_2 uptake rate ($\mu mol\ m^{-2}\ s^{-1}$)	Total daily net CO_2 uptake ($mmol\ m^{-2}\ day^{-1}$)	Reference
Pereskioideae			
Maihuenia poeppigii (leaf)	4.3	159	Nobel and Hartsock (1987)
Pereskia aculeata (leaf)	4.7	130	"
Pereskia grandifolia (leaf)	6.0	202	"
Opuntioideae			
Austrocylindropuntia subulata (leaf)	3.2	91	Nobel and Hartsock (1986a)
Opuntia acanthocarpa	5.5	187	Nobel et al. (1991)
O. basilaris	6.2	241	Hanscom and Ting (1978)
O. erinacea	5.3	146	Littlejohn (1983)
O. ficus-indica	18.0	698	Cui et al. (1993); Cui and Nobel (1994)
O. humifusa	8.4	283	Koch and Kennedy (1980)
O. phaeacantha	3.2	—	Nisbet and Patten (1974)
O. polyacantha	2.9	107	Gerwick and Williams (1978)
O. stricta	13.5	506	Osmond et al. (1979)
Pereskiopsis porteri (leaf)	2.4	96	Nobel and Hartsock (1986a)
Quiabentia chacoensis (leaf)	3.1	103	"
Cactoideae			
Carnegiea gigantea	—	192	Nobel and Hartsock (1986a)
Cereus validus	5.8	181	Nobel et al. (1984)
Cryptocereus anthonyanus	3.0	60	Nobel and Hartsock (1990)
Echinocereus engelmannii	2.9	98	Nobel et al. (1991)
Epiphyllum oxypetalum	2.2	46	Nobel and Hartsock (1990)
E. pittieri	2.0	61	"
Ferocactus acanthodes	6.0	164	Nobel and Hartsock (1986a)
Hylocereus undatus	5.1	214	Raveh et al. (1995)
Mammillaria dioica	5.5	91	Nobel (1978); Nobel and Hartsock (1986a)
Pachycereus pringlei	6.5	297	Franco-Vizcaíno et al. (1990)
Rhipsalis houlletiana	3.0	104	Nobel and Hartsock (1990)
R. rhombea	2.1	59	"
Schlumbergera truncata	3.2	65	"
Stenocereus queretaroensis	11.2	317	Nobel and Pimienta-Barrios (1995); Pimienta-Barrios and Nobel (1998)

Data are restricted to those expressed on a unit surface area basis and under essentially optimal environmental conditions. For a more complete coverage of the earlier literature, see Nobel (1988). Values are for stems unless otherwise indicated.

Usually there is no net CO_2 uptake during the middle of the daytime, but rather a slight loss occurs (Phase III; Fig. 4.1); at this time the acids accumulated the previous night are decarboxylated, and the CO_2 released within the plant is refixed in the stems using Rubisco. The high internal concentration from this released CO_2 causes the daytime leakage of CO_2 from the stems. Stomates tend to reopen in late afternoon after stem temperatures have decreased, leading to net uptake and fixation of CO_2 using Rubisco (Phase IV; Fig. 4.1).

Maximal instantaneous rates of net CO_2 uptake are about 3 $\mu mol\ m^{-2}\ s^{-1}$ for *Opuntia polyacantha,* which is native to the central United States, 8 $\mu mol\ m^{-2}\ s^{-1}$ for *O. humifusa,* the mostly widely distributed native opuntia in the United States, and 18 $\mu mol\ m^{-2}\ s^{-1}$ for *O. ficus-indica,* the most widely cultivated cactus worldwide (Fig. 4.1). Species in the largest subfamily, Cactoideae, also have net CO_2 uptake by stems at night in the CAM mode. Maximal nighttime net CO_2 uptake rates are high for *Cereus validus, Ferocactus acanthodes, Mammillaria dioica,* and *Pachycereus*

pringlei (average about 6 μmol m^{-2} s^{-1}) and *Stenocereus queretaroensis* (11 μmol m^{-2} s^{-1}; Table 4.1). Maximal net CO_2 uptake rates for epiphytic cacti, such as species of *Cryptocereus, Epiphyllum, Rhipsalis,* and *Schlumbergera,* are much lower (2–3 μmol m^{-2} s^{-1}), although the cultivated, shade-tolerant, vinelike, hemiepiphytic cactus *Hylocereus undatus* can have maximal rates of 5 μmol m^{-2} s^{-1} (Table 4.1). Values for total daily net CO_2 uptake under optimal environmental conditions are consistent with maximal instantaneous rates of net CO_2 uptake for cacti. Among the cacti investigated, maximal total daily net CO_2 uptake occurs for opuntias (698 mmol m^{-2} day^{-1} for *O. ficus-indica* and 506 mmol m^{-2} day^{-1} for *Opuntia stricta*) and *S. queretaroensis* (317 mmol m^{-2} day^{-1}; Table 4.1).

Water-Use Efficiency

The importance of nocturnal stomatal opening and the accompanying net CO_2 uptake with regard to ecological or agronomic success of cacti relates less to improving CO_2 acquisition than to reducing water loss. In particular, air and stem temperatures are lower at night, which leads to a lower concentration of water vapor in the stem and hence less water loss for a given degree of stomatal opening; this is important in arid regions (less than 250 mm annual rainfall) or semiarid regions (250 to 450 mm annual rainfall). The ratio of CO_2 fixed to water loss in transpiration is termed the water-use efficiency, which is an important benefit:cost index for assessing the gas-exchange performance of plants. For stems of cacti under favorable environmental conditions with predominantly nocturnal net CO_2 uptake, approximately 10 mmol of CO_2 is taken up per mol of water transpired over a 24-hour period. This water-use efficiency is about three times higher than for highly efficient C_4 species such as *Zea mays* (maize) and *Saccharum officinarum* (sugarcane) and five times higher than for highly efficient C_3 species such as *Medicago sativa* (alfalfa) and *Triticum aestivum* (wheat; Nobel 1991).

To better understand the reason water loss is reduced at night due to lower temperatures, consider the water-vapor concentration at saturation (as essentially occurs within the stems of cacti). The saturation water vapor content of air increases nearly exponentially with increasing temperature, whereas the water content of the ambient air surrounding a plant remains relatively constant unless the weather abruptly changes. In particular, air saturated with water vapor at 15°C, which can represent nighttime temperatures, contains 12.8 g m^{-3}; at 25°C, which can represent daytime temperatures, air saturated with water vapor contains 23.1 g m^{-3} (Nobel 1999). If the ambient air contains 8.0 g water m^{-3}, which corresponds to 46% relative humidity at 20°C, the leaf-to-air difference in water vapor concentration (the force leading to water loss by transpiration) is 12.8 – 8.0 or 4.8 g m^{-3} at 15°C and 23.1 – 8.0 or 15.1 g m^{-3} at 25°C, which is threefold greater at the higher temperature. Therefore, transpiration would be threefold greater at a daytime temperature of 25°C than for the same degree of stomatal opening at night at 15°C. This is a key feature for the water-conserving nature of CAM used by cacti in arid and semiarid regions. In particular, because tissue temperatures in the field tend to average about 10°C lower at night than during the daytime, CAM plants tend to lose only 20 to 35% as much water for the same degree of stomatal opening during the principal periods of net CO_2 uptake as do C_3 or C_4 plants.

Net CO_2 Uptake: Stems

Net CO_2 uptake, which has been determined per unit surface area for about 20 species of cacti (Table 4.1), depends on several environmental factors. The three key environmental factors for drought-enduring plants are temperature, soil moisture, and the solar irradiation absorbed by photosynthetic pigments, i.e., the photosynthetic photon flux (PPF), which represents wavelengths of 400 to 700 nm. The response of net CO_2 uptake by *Opuntia ficus-indica,* the most widely studied cactus, to these three variables (Fig. 4.2) is important for predicting its productivity under any environmental condition and serves as a model for assessing the net CO_2 uptake, and hence the potential biomass productivity, of other cacti.

Temperature

The daily pattern and the magnitude of total net CO_2 uptake by *O. ficus-indica* (Fig. 4.1) mainly reflect nocturnal temperatures. In particular, PEPCase is more important for the initial binding of CO_2 than is Rubisco. The optimal mean nocturnal temperature is relatively low, 15°C (Fig. 4.2A). Moreover, substantial net CO_2 uptake occurs at 0°C for *O. ficus-indica,* and *O. humifusa* can even have substantial net CO_2 uptake at air temperatures of –5°C (Nobel and Loik 1990). Thus, low nighttime temperatures are not disadvantageous for net CO_2 uptake by these cacti, whereas high nighttime temperatures, such as those above 30°C (Fig. 4.2A), can lead to appreciable stomatal closure and hence limited net CO_2 uptake.

Although most cacti examined have a low temperature optimum (near 15°C) for net CO_2 uptake, epiphytic cacti native to the tropical areas of the Americas are subject to much higher mean nocturnal temperatures for most of the year and can acclimate to higher stem temperatures for their PEPCase activity. For instance, *Hylocereus undatus* has

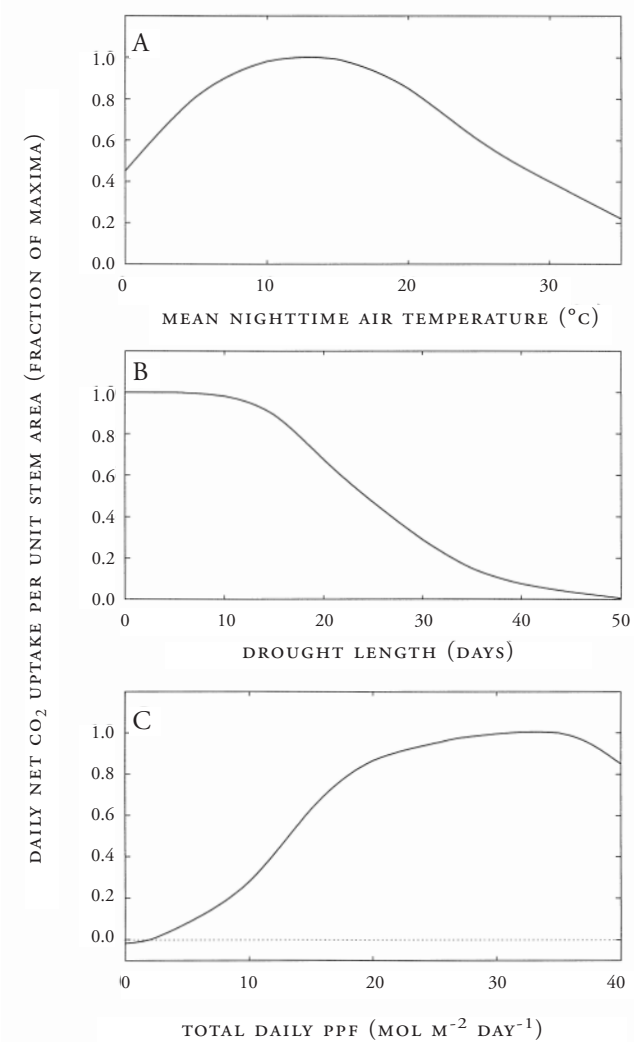


Figure 4.2. Influence of three environmental factors on net CO_2 uptake by *O. ficus-indica* over 24-hour periods: (A) temperature, in particular the mean nighttime air temperature, which was generally within 1°C of the temperature in the middle of the chlorenchyma; (B) water availability, measured by drought length, defined as when the stem water potential becomes less than the soil water potential adjacent to the roots, preventing plant water uptake; and (C) solar irradiation that can be absorbed by photosynthetic pigments, known as PPF (wavelengths of 400 to 700 nm, i.e. blue to red). Except when that specific factor was varied, the plants were under essentially optimal conditions of nighttime temperatures near 15°C, wet soil, and a total daily PPF of about 25 mol m^{-2} day^{-1} incident on the cladode surfaces. Data are from Nobel and Hartsock (1983, 1984, 1986b), Nobel and Israel (1994), and Israel and Nobel (1995).

maximum nocturnal net CO_2 uptake at 25°C (Raveh et al. 1995). Just as high temperatures have relatively little influence on the survival and distribution of cacti, high daytime air and stem temperatures are not critical for daily net CO_2 uptake by cacti (Nobel 1988). Although the mean nighttime temperature is more useful for quantifying nocturnal net CO_2 uptake, the minimum nighttime temperature (usually 3°C to 6°C lower than the mean temperature) is more readily available from weather records and can be correlated with net CO_2 uptake as well.

Water

As the water content of the soil declines and its water potential decreases below that of the plant, thermodynamic theory predicts that water will move from the plant to the soil (Nobel 1999). Water is also continually being lost from the shoot of a plant to the atmosphere. The inevitable loss of stem water as the soil dries inhibits cellular processes that lead to net CO_2 uptake (Fig. 4.2B). In particular, little change in net CO_2 uptake occurs during the first 7 days of drought for *O. ficus-indica* because of the water stored in its cladodes and the high water-use efficiency of the CAM pathway. Daily net CO_2 uptake then halves over the next 17 days of drought and becomes near zero at 50 days (Fig. 4.2B); the gradual decline in part reflects the inherently low transpiration rates resulting from a low stomatal frequency and a thick cuticle. The response to soil water content can be used to devise irrigation schedules for *O. ficus-indica* and other cultivated cacti in arid and semiarid regions and to discern seasonal patterns of net CO_2 uptake for native cacti in deserts.

PPF

Net CO_2 uptake is negative for stems maintained continually in the dark (Fig. 4.2C), as only respiration occurs under such circumstances because photosynthesis requires light. Net CO_2 uptake increases as the total daily PPF increases and becomes half-maximal at about 13 mol m^{-2} day^{-1} for *O. ficus-indica* (Fig. 4.2C; because most CO_2 uptake occurs at night, data on the light responses of cacti are generally based on the total daily PPF). Net CO_2 uptake approaches light saturation at about 30 mol m^{-2} day^{-1}, which is approximately half the total daily PPF incident on a horizontal surface on a clear day with the sun passing overhead at noon (the instantaneous PPF is then about 2,000 µmol m^{-2} s^{-1}) but about equal to that incident on a vertical surface of a cactus stem facing east or west on such a day (Nobel 1988). For the shade-tolerant hemiepiphyte *Hylocereus undatus,* on the other hand, net CO_2 is half-maximal at only 4 mol m^{-2} day^{-1}, maximal at 20 mol m^{-2} day^{-1}, and is 40% of maximal at 30 mol m^{-2} day^{-1} (Raveh et al. 1995). For the holoepiphyte *Schlumbergera truncata,* photosynthesis is inhibited at even lower light levels, with daily net CO_2 uptake being 19% lower for plants exposed to a total daily PPF of 17 mol m^{-2} day^{-1} than for those exposed to 9 mol m^{-2} day^{-1} (Nobel and Hartsock 1990). Indeed, epiphytic cacti generally do better under shaded

conditions, both in the field and under cultivation (Mizrahi et al. 1997).

One reason that unshaded nonepiphytic cacti generally do not exhibit chronic photoinhibition (damage to the light-dependent processes of photosynthesis due to excess PPF; Taiz and Zeiger 1998) is that most of their photosynthetic surfaces are vertical and thus not perpendicular to the incoming PPF. Spines and pubescence can also create considerable shading for the stems of many cacti; in particular, the apices of certain ecotypes of *Ferocactus acanthodes* are exposed to only 10% of the incoming PPF (Nobel 1980). The recycling of internal CO_2 can also help prevent chronic photoinhibition by maintaining photosynthetic activity, thereby avoiding harmful effects of absorbed light (Nobel 1988). Although chronic photoinhibition is uncommon in cacti, dynamic photoinhibition, which results in a temporary decrease in photosynthetic efficiency due to the radiationless dissipation of absorbed PPF (Taiz and Zeiger 1998), is common, especially during drought and in the late afternoon under favorable conditions, when endogenous CO_2 levels are low (Adams et al. 1989; Barker and Adams 1997). The excess PPF that cannot be used in photosynthesis is dissipated in reactions involving xanthophylls and other carotenoids. For *O. macrorhiza,* the concentrations of carotenoids in a cladode surface correlate with orientation, the greatest concentrations occurring in cladodes facing south or west, which are the surfaces that receive the most sunlight in the afternoon (Barker and Adams 1997).

Influences of plant architecture on the interception of PPF differ for the massive opaque stems of cacti that exhibit CAM, compared with the relatively thin, flat leaves of C_3 and C_4 species, for which light incident on either surface can be distributed throughout the leaf. For instance, the face of a cladode of a platyopuntia or the side of a roughly spherical barrel cactus facing poleward can receive far less than optimal total daily PPF when the opposite equatorially facing side is approaching PPF saturation of daily net CO_2 uptake. Hence, because some of the plant's surfaces face away from direct sunlight essentially the entire day, some face sunward, and others face in intermediate directions, net CO_2 uptake by whole plants of such species under unshaded conditions tends to increase up to full sunlight. In other words, because of the architecture of cacti, part of the stems, and hence the plants themselves, are always light-limited with respect to CO_2 uptake. Moreover, the phototropism of *O. leucotricha* mentioned in the Introduction also occurs for *O. ficus-indica,* as newly developing cladodes can rotate 16° to become more perpendicular to a unidirectional light beam (Nobel 1982b).

In the field, cladodes tend to be favorably oriented to intercept more PPF and to have more net CO_2 uptake (Fig. 4.2C) and hence more biomass productivity. Such cladode orientation is dependent on the latitude of the plants and the timing of cladode initiation. For instance, because of the path of the sun in the sky, an east-west orientation tends to be favored for plants close to the equator and decreases with distance from the equator. Cladodes initiated during the winter tend to have a north-south orientation, whereas cladodes that are initiated during the summer face east-west. Because daughter cladodes of various platyopuntias tend to be oriented in the same plane as the underlying mother cladodes, orientation tendencies can be observed at the whole plant level (Nobel 1982c, 1988).

Nutrients and Salinity

Net CO_2 uptake, and thus nocturnal acid accumulation, for the stems of cacti can also be affected by nutrient levels in the soil and hence in the stem (Nobel 1989). Of the nutrients investigated, nitrogen has the greatest positive effect on net CO_2 uptake. For *O. ficus-indica,* nocturnal net CO_2 uptake, as reflected in increases in tissue acidity, more than doubles as the nitrogen level in the chlorenchyma increases from 1% of the dry mass to over 2% (Nobel 1983). Among nine other species of cacti for which the nitrogen content in the chlorenchyma ranges from 1.0% to 2.5% of the dry mass, maximal nocturnal acid accumulation increases with average nitrogen content (Nobel 1983). Low stem nitrogen content may be one of the reasons that *Stenocereus queretaroensis* has a lower net CO_2 uptake than do most other cultivated cacti (Nobel and Pimienta-Barrios 1995). For *O. engelmannii* and *O. rastrera,* dry mass increases 73% when fields are fertilized with 160 kg nitrogen per hectare (Nobel et al. 1987). Other nutrients that show a positive effect on net CO_2 uptake by cacti are potassium, phosphorous, and boron (Nobel et al. 1987; Nobel 1989).

Soil salinity has a negative affect on net CO_2 uptake. Net CO_2 uptake for *O. ficus-indica* decreases by about 50% after exposure to a 150 mM NaCl solution and 83% after exposure to a 200 mM solution for 10 weeks (Fig. 4.3). Longer term exposure to high concentrations of NaCl has an even more profound effect, with exposure to a solution of 100 mM for six months causing a net CO_2 efflux for *O. ficus-indica* (Hatzmann et al. 1991). The concentration of NaCl in the chlorenchyma also correlates with net CO_2 uptake, because CO_2 uptake halves as the sodium level in the chlorenchyma increases from 20 ppm by dry mass to 300 ppm for *O. ficus-indica* (Nobel 1983) and from 10 to 80 ppm for *Cereus validus* (Nobel et al. 1984). The latter tissue level

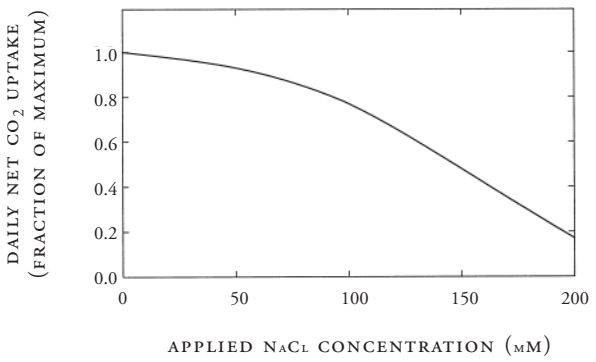


Figure 4.3. Influence of a 10-week application of NaCl solutions on daily net CO_2 uptake for cladodes of *O. ficus-indica.* Plants were grown in 50% Hoagland solution, plus the indicated NaCl concentration. Data are from Nerd et al. (1991).

can be caused by exposing *C. validus* to 400 mM NaCl for 16 days. When *O. humifusa* is exposed to 150 mM NaCl for 6 weeks, total daily net CO_2 uptake is reduced 94% for plants from inland populations but 71% for plants from the marine strand that are exposed to higher soil salinity in their native habitat (Silverman et al. 1988).

Atmospheric CO_2

As the CO_2 concentration in the atmosphere is increased, the driving force for CO_2 entry into cacti, and hence net CO_2 uptake, tends to increase. Yet C_3 plants, when exposed to doubled atmospheric CO_2 concentrations, often acclimate to the new conditions after a period of months, leading to less enhancement than observed initially (Drennan and Nobel 2000). All four species of cacti that have been exposed to a doubled atmospheric CO_2 concentration have shown increases in both total daily net CO_2 uptake and biomass productivity. For instance, the biomass increase over a 12-month period is 30% greater for *Ferocactus acanthodes* at a doubled compared with the current atmospheric CO_2 concentration (Nobel and Hartsock 1986c). For *Hylocereus undatus,* total daily net CO_2 uptake is 34% higher under the doubled atmospheric CO_2 concentration (Raveh et al. 1995), and for *Stenocereus queretaroensis* it is 36% higher (Nobel 1996).

Opuntia ficus-indica is the most studied CAM species with respect to effects of elevated atmospheric CO_2 concentrations (Drennan and Nobel 2000). Its total daily net CO_2 uptake for terminal cladodes can be enhanced 41 to 61% by doubling the atmospheric CO_2 concentration (Cui et al. 1993). Its biomass increase over a 12-month period is 40% greater under a doubled atmospheric CO_2 concentration than under the current one (Nobel and Israel 1994). Other responses of *O. ficus-indica* to elevated atmospheric CO_2 concentrations include thicker cladodes, a thicker chlorenchyma, increased chlorenchyma cell length, a decrease in PEPCase per unit cladode area, a decrease in stem nitrogen concentration, a decreased stomatal frequency, an increased root:shoot ratio, increased root cell length, and a 60 to 70% increase in water-use efficiency (Cui et al. 1993; Luo and Nobel 1993; North et al. 1995; Drennan and Nobel 2000).

Net CO_2 Uptake: Fruits

CO_2 uptake for fruits of cultivated platyopuntias follows a typical CAM pattern (Fig. 4.1), although maximum instantaneous net CO_2 uptake rates and total daily net CO_2 uptake (Table 4.2) are only 10 to 40% as high as for stems (Inglese et al. 1994; Nobel and De la Barrera 2000). In particular, CO_2 uptake rates for young fruits of platyopuntias are similar to those for stems of uncultivated cacti (Table 4.1). The daily net CO_2 uptake by young fruits accounts for only 6 to 15% of their total daily dry-mass gain (Table 4.2). The contribution to dry-mass gain decreases with fruit age, reflecting decreases in Rubisco and PEPCase activity and in chlorophyll content (Inglese et al. 1994). In contrast, during the first two weeks after initiation, cladodes of *Opuntia ficus-indica* have a daily net CO_2 loss, but at four weeks they have a net CO_2 gain that is similar to that of their underlying mature cladodes (Wang et al. 1997). Thus, cladodes make the transition from a carbohydrate sink to a carbohydrate source at an early age, whereas fruits become more of a carbohydrate sink as they mature.

Because the contribution of net CO_2 uptake to the dry-mass gain of platyopuntia fruits is small (Table 4.2), during their development fruits must receive considerable carbohydrates from underlying mature cladodes via the phloem (Inglese et al. 1994; Wang et al. 1997; Nobel and De la Barrera 2000). However, the importance of the phloem to fruits lies not only in the supplying of solutes. Platyopuntia fruits have water potentials that are higher (less negative) than those of their underlying cladodes, indicating that water cannot flow passively in the xylem from the cladodes to the fruit (Nobel et al. 1994), as occurs for most developing organs (Nobel 1999). Rather, the phloem is responsible for water transport into the fruits of platyopuntias (Nobel et al. 1994), much as it is for 2-week-old cladodes of *O. ficus-indica* (Wang et al. 1997). Moreover, the osmotic pressure of the phloem sap entering the fruits of *O. ficus-indica* is relatively low (0.94 MPa) compared with the phloem sap in other plants (Nobel et al. 1994). The fruits transpire over 60% of the imported water, leading to a large buildup of solutes (Nobel and De la Barrera 2000). To maintain higher water potentials than their un-

TABLE 4.2
Net CO_2 uptake and its contribution to dry-mass gain for young fruits of six platyopuntia species

Species	Maximum net CO_2 uptake rate ($\mu mol\ m^{-2}\ s^{-1}$)	Total daily net CO_2 uptake ($mmol\ m^{-2}\ day^{-1}$)	Percent daily dry mass gain due to net CO_2 uptake (%)
N. cochenillifera	2.9	95	6.3
O. ficus-indica	4.9	121	10.9
O. megacantha	4.8	85	8.8
O. robusta	6.3	155	9.8
O. streptacantha	4.8	114	8.3
O. undulata	5.9	174	14.8

Data are for fruits midway between floral bud appearance and fruit maturation and are from Nobel and De la Barrera (2000).

derlying cladodes, the sucrose, other sugars, and amino acids delivered by the phloem to the fruits (Wang and Nobel 1995) are probably polymerized into osmotically inactive proteins, mucilage, and starch (Nobel and De la Barrera 2000). This allows the fruits to continue receiving water and solutes from the phloem, thus increasing their sugar and starch content.

Productivity Responses to Environmental Factors

The curves developed for environmental responses of net CO_2 uptake (Fig. 4.2) were obtained in the laboratory, where one factor at a time was varied under controlled conditions. However, variations in air temperature, drought duration, and total daily PPF occur simultaneously in the field. For instance, to examine the effect of elevation on net CO_2 uptake and biomass productivity, the decreasing air temperature, generally increasing water availability, and variable changes in PPF with increasing elevation must all be considered.

Environmental Productivity Index

One method of dealing with the simultaneous variation of environmental factors is to multiply the influence of the three main environmental factors (Fig. 4.2) on net CO_2 uptake:

Eq. 4.1 Environmental Productivity Index (EPI) =
Fraction of maximal total daily net CO_2 uptake =
Temperature Index × Water Index × PPF Index

where each component index ranges from zero (the point at which that factor completely inhibits total daily net CO_2 uptake per unit area) to one (where that factor is optimal for net CO_2 uptake; Nobel 1984, 1988, 1999). Thus, each component index is normalized to one under the optimal conditions for that environmental factor. EPI can be used to estimate the fraction of maximal total daily net CO_2 uptake per unit area expected for certain prevailing conditions and should be calculated for various areas on the plant. This fraction is multiplied by the total daily net CO_2 uptake per unit area under optimal conditions to predict the actual daily net CO_2 uptake. The total daily net CO_2 uptake per plant can be obtained by the actual uptake values per area times the respective areas into which the plant has been divided. The total daily net CO_2 uptake per unit ground area can be obtained from the total net CO_2 uptake per plant and the ground area per plant. Finally, CO_2 uptake can be numerically converted to biomass, assuming that the CO_2 is converted to carbohydrate (30 g mol^{-1}) or some other biomass equivalent, leading to a biomass productivity in kg m^{-2} day^{-1}. This daily biomass productivity is then summed up over a year to obtain the annual productivity, which is conventionally expressed in tons (1,000 kg) dry mass $hectare^{-1}$ $year^{-1}$ (Nobel 1991).

Application of EPI to a Barrel Cactus

For *Ferocactus acanthodes* in the northwestern Sonoran Desert, the Temperature Index approaches 1.00 for the moderately cool parts of the year in late autumn and the spring, as the summer is too hot and the winter is too cold for maximal net CO_2 uptake by this cactus (Fig. 4.4A). The Water Index approaches 1.00 for the rainy periods in late summer and the early winter (Fig. 4.4B). The seasonal variation in the PPF Index averaged over the plant surface (Fig. 4.4C) reflects the variation in the sun's trajectory with the time of year, being lowest in the winter and highest near the early summer. The product of these three indices, EPI,

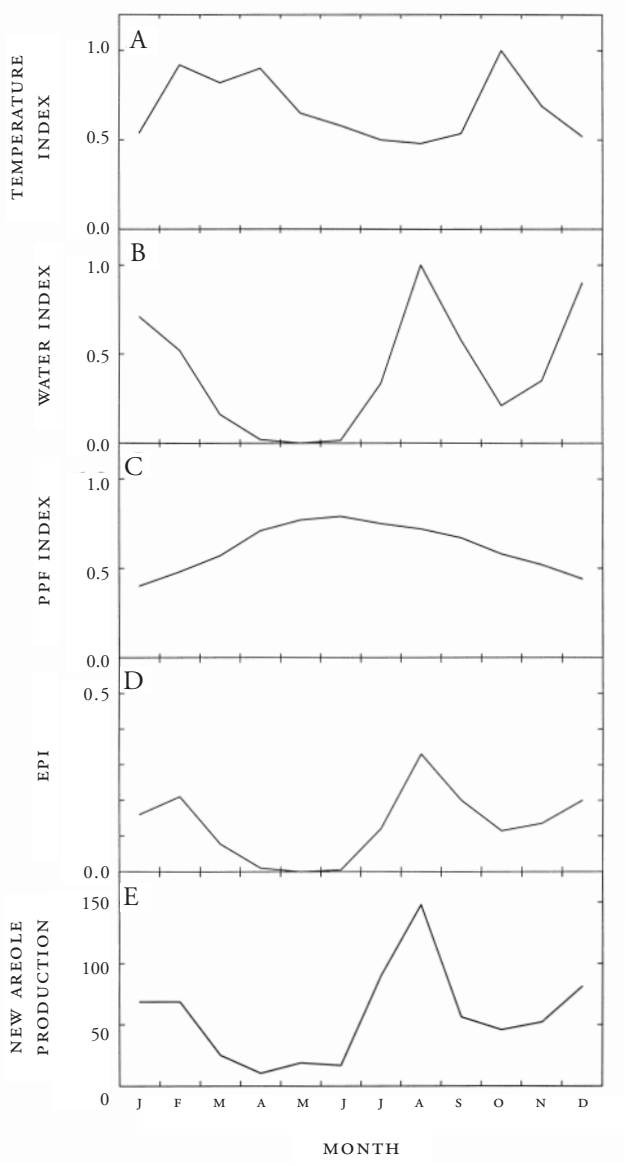


Figure 4.4. Monthly variation in component indices, EPI, and production of new areoles by *Ferocactus acanthodes* in the northwestern Sonoran Desert: (A) Temperature Index, (B) Water Index, (C) PPF Index (including effects of clouds), (D) Environmental Productivity Index (see Eq. 4.1.), and (E) production of new areoles. Data for the areoles are from 33 plants examined monthly. Adapted from Nobel (1986).

reaches a peak in late summer (Fig. 4.4D), which coincides with the peak in monthly production of new areoles (Fig. 4.4E). The overriding importance of the Water Index is clearly evident in the seasonal pattern for EPI and areole production by this cactus in the Sonoran Desert.

Application of EPI to a Cultivated Platyopuntia

Besides relating growth to net CO_2 uptake under natural conditions, EPI can also be used to predict how well a cultivated cactus such as *Opuntia ficus-indica* may grow in a particular region (Garcia de Cortázar and Nobel 1991). The Temperature Index can be used to evaluate maritime or elevational influences on net CO_2 uptake for a particular site. The Water Index can be used to quantify the influence of the timing of irrigation on net CO_2 uptake. However, the component index that has had the greatest influence on agronomic practices for *O. ficus-indica* is the PPF Index, which can be directly related to plant spacing. In particular, the nonlinear response to total daily PPF for net CO_2 uptake by individual stem surfaces (Fig. 4.2C) suggests that excessive shading should be avoided, i.e., when the stem area index—total area of both sides of all cladodes per unit ground area—becomes very high, the average PPF incident on the cladodes decreases, leading to less total daily net CO_2 uptake per unit cladode area (Fig. 4.5). However, although spacing plants at large distances maximizes net CO_2 uptake per plant, it leads to little net CO_2 per unit ground area. Computer models dividing the stems of *O. ficus-indica* into many surfaces facing in different directions and using hourly values for PPF throughout a year have indicated an optimal spacing for net CO_2 uptake per unit ground area (Garcia de Cortázar et al. 1985; Garcia de Cortázar and Nobel 1991). In particular, the stem area index should be about 4 to 5 for optimal biomass productivity (Fig. 4.5). Although some modification of such close spacing is necessary for management practices, such as picking of fruit, the simulation modeling indicates that much closer spacing than had been traditionally used in various locations greatly enhances biomass productivity per area.

Based on calculations using EPI, experimental field plots were established to ascertain the maximal productivity of *O. ficus-indica* under environmental conditions approaching those optimal for net CO_2 uptake. To meet those conditions, sites were chosen with moderate nighttime temperatures (and hence a high Temperature Index) and with nutrient-rich soils. The plants were optimally spaced or pruned to keep the stem area index at 4 to 5 and were irrigated to maintain the Water Index near 1.00. Under such conditions, *O. ficus-indica* and *O. amyclaea* had a annual biomass productivities of 45 to 50 tons dry mass hectare^{-1} year^{-1} (Garcia de Cortazar and Nobel 1992; Nobel et al. 1992). Such extremely high biomass productivities are exceeded by those of only a few cultivated C_3 and C_4 species. Indeed, the annual biomass productivities are 38 tons hectare^{-1} year^{-1} for the four most productive C_3 crops, 41 tons hectare^{-1} year^{-1} for the four most productive C_3 trees, and 56 tons hectare^{-1} year^{-1} for the four most productive C_4 crops (Nobel 1991). Although most cacti are relatively slow growing, with modest net CO_2 uptake, certain

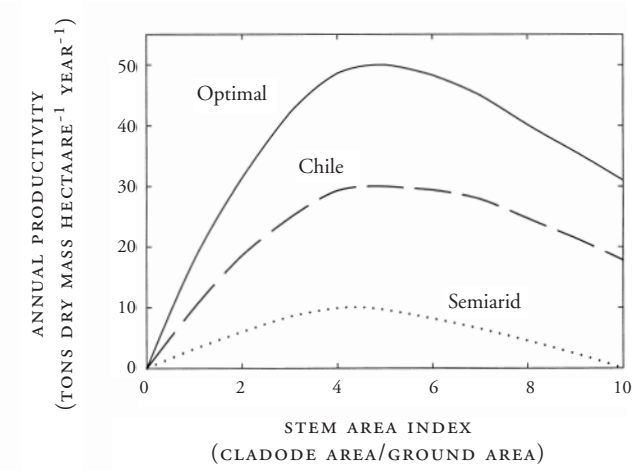


Figure 4.5. Biomass productivity for *O. ficus-indica* as a function of plant spacing as quantified by the stem area index (SAI). *Optimal* refers to conditions that include irrigation, leading to a Water Index of 1.00; *Chile* refers to natural conditions near Santiago, Chile; *Semiarid* refers to conditions that are discussed in the text. Data are adapted from Garcia de Cortázar et al. (1985); Garcia de Cortázar and Nobel (1991); and Nobel (1991).

opuntias have great potential for biomass productivity and could even be used for sequestering massive amounts of carbon, an international goal for mitigating the increasing atmospheric CO_2 concentrations and the accompanying global climatic warming.

Besides indicating conditions for maximal productivity, EPI can also be used to estimate productivity under more typical field conditions. For instance, predictions can be made for a region near Santiago, Chile, where *O. ficus-indica* is grown without irrigation for fruit production (Fig. 4.5). Moreover, the stem area index for *O. ficus-indica* may be near 2 to allow pathways in the field for plant maintenance and harvesting of fruits or cladodes, which would lead to 62% of maximal net CO_2 uptake per unit ground area (Fig. 4.5). A site chosen for the cultivation of *O. ficus-indica* might not have ideal temperatures, at least for certain seasons. Actually, total daily CO_2 uptake does not vary tremendously with mean nighttime temperature, being within 40% of the maximal values for mean nighttime temperatures from 2°C to 25°C (Fig. 4.2A), and so the Temperature Index may average 0.80 on an annual basis. If the cultivation site is semiarid with two wet periods per year, the Water Index might average 0.25 on an annual basis. Hence, for a stem area index of 2, EPI may average (0.62)(0.80)(0.25) or 0.12. If 50 tons dry mass hectare^{-1} year^{-1} is taken as the maximum productivity, then the predicted productivity for the site would be (0.12)(50) or 6 tons hectare^{-1} year^{-1} (Fig. 4.5), which is representative of biomass productivities of *O. ficus-indica* in semiarid regions without irrigation. Moreover, cacti, with their high water-use efficiency, have a distinct advantage over C_3 and C_4 species in such regions; e.g., *O. ficus-indica* can be cultivated in regions with too little soil moisture for *Zea mays* and other such crops.

Survival

Temperature

Temperature influences every process in plants, from photosynthesis and respiration to growth and survival. With respect to survival, low temperatures are more critical with regard to the distribution of native species of cacti and the cultivation of opuntias than are high temperatures. For instance, the northern limits of the columnar cacti *Carnegiea gigantea, Lophocereus schottii,* and *Stenocereus thurberi* in Arizona are dictated by episodic low temperatures (Turnage and Hinckley 1938; Nobel 1988). In particular, these three species can be killed by stem temperatures of −7 to −10°C, similar to the lethal temperatures for cultivated arborescent species such as *Opuntia ficus-indica* and *Stenocereus queretaroensis* (Table 4.3). In contrast, certain lower growing species can tolerate about −20°C, e. g., *Coryphantha vivipara, Opuntia humifusa,* and *Pediocactus simpsonii* (Table 4.3), which are all native to regions in the northern United States that receive appreciable snowfall. Moreover, *Opuntia fragilis,* which occurs north of 56° north latitude in western Canada, can tolerate extremely low stem temperatures of −48°C (Loik and Nobel 1993).

Cacti that tolerate extremely low temperatures exhibit superior ability for low-temperature hardening (increase in the tolerance of subzero temperatures as the ambient temperature is gradually decreased over a period of weeks; Nobel 1988). Cladodes with lower water content tend to tolerate lower temperatures (Nobel 1988; Loik and Nobel 1991; Nobel et al. 1995). For example, tissue water content for *O. humifusa* (Fig. 4.6), which is native to southeastern Canada and the eastern United States, generally decreases by 35% in the winter, and winter kill is limited to plants with greater water content, suggesting that cold tolerance for cacti might depend on increases in osmotic pressure (Koch and Kennedy 1980). In fact, when day/night temperatures decrease from 30/20°C to 10/0°C, the osmotic pressure for *O. humifusa* increases four times more than do the osmotic pressures for the subtropical and less freezing-tolerant *O. ficus-indica* and *O. streptacantha,* due to a greater synthesis of simple sugars and the production of mannitol within the cells of *O. humifusa* (Goldstein and Nobel 1994).

Because the cellular contents of cacti would freeze at −1 to −2°C based on their osmotic pressure and the relation

TABLE 4.3
Extreme temperatures that can be tolerated by cacti

Species	Low temperature tolerance (°C)	High temperature tolerance (°C)
Ariocarpus fissuratus	—	70
Carnegiea gigantea	−9	65
Coryphantha vivipara	−22	68
Denmoza rhodacantha	−11	—
Epithelantha bokei	—	64
Eriosyce ceratistes	−11	—
Ferocactus acanthodes	−9	69
F. covillei	−7	71
F. viridescens	−7	69
F. wislizenii	−9	70
Lophocereus schottii	−7	68
Mammillaria dioica	—	69
M. lasiacantha	—	67
Opuntia acanthocarpa	—	65
O. basilaris	—	66
O. bigelovii	−8	64
O. chlorotica	—	69
O. ficus-indica	−10	70
O. fragilis	−48	—
O. humifusa	−25	—
O. polyacantha	−18	—
O. ramosissima	−5	68
Pediocactus simpsonii	−19	—
Stenocereus queretaroensis	−9	—
S. thurberi	−10	68
Trichocereus candicans	−9	—
T. chilensis	−9	—

Data are based on the uptake of a vital dye (neutral red) by cells in tissues exposed to the extreme temperature for 1 hour for plants that have been gradually adjusted to low or high day/night air temperatures. The indicated temperature will cause immediate death of over half of the cells, generally leading to death of the plants. Data are from Nobel (1982a, 1988, 1996); Smith et al. (1984); Nobel et al. (1986); and Loik and Nobel (1993).

between freezing-point depression and osmotic pressure (Nobel 1999), the mechanism of low temperature damage to cacti is not due to the wholesale freezing of cellular water (Nobel 1988). Rather, the initial ice crystals form outside the cells, following a super cooling of the stem (lowering of the stem temperature below the freezing point of the cell sap). Intracellular water molecules are then progressively transferred to the growing extracellular crystals, leading to the shrinkage of protoplasts and the desiccation of the cells. The continuing dehydration of the cells affects their membranes and enzymes, leading to disruption of metabolic processes and eventual cellular death.

How many genes are involved in the multitude of factors leading to greater tolerance of low temperature? This is an important question for breeders and biotechnologists (Chapter 15) dealing with commercialized cacti, as domesticated cultivars tend to have a poorer tolerance of low temperatures compared with many native species (Russell and Felker 1987; Table 4.3). Indeed, one of the major limitations in the expansion of the regions where *O. ficus-indica* and other platyopuntias can be cultivated is episodic low temperatures, suggesting that global climate warming will be favorable to increased cultivation of such cacti (Nobel 1996).

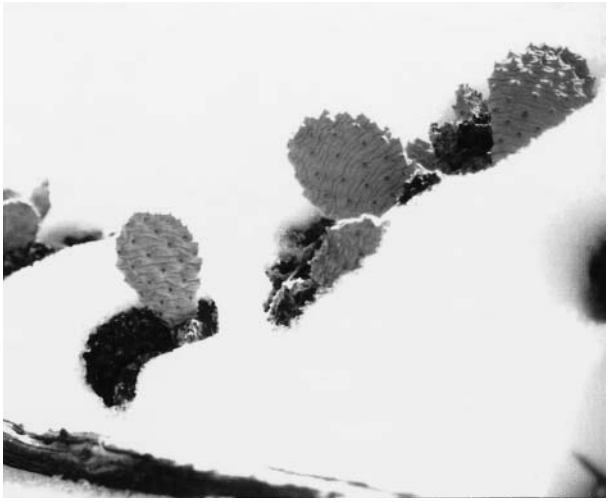


Figure 4.6. *Opuntia humifusa* on a snow-covered hillside in Ontario, Canada. The wrinkled appearance of the cladodes is due to dehydration, a response to exposure to low temperatures. Photograph is courtesy of Michael E. Loik.

Although low temperature tolerance has major effects on the natural distribution of cacti and the regions where they can be successfully cultivated, high temperatures are generally not a major limiting factor. For instance, of the 17 species that have been assessed quantitatively, the tolerated high temperature averages 68°C (Table 4.3). This is an incredibly high temperature to survive, as metabolic processes are severely disrupted at 55 to 60°C for most plants (Nobel 1988). Tolerated high temperatures are remarkably similar among stem types, being essentially the same for barrel cacti, columnar cacti, and opuntias (Table 4.3). The cellular and genetic bases for the high-temperature tolerance of cacti have not been described. In any case, high-temperature damage generally occurs for cacti where the stem contacts the soil, which can have surface temperatures of up to 70°C in deserts (Nobel 1988). Hence nurse plants are often important for ensuring the establishment of cactus seedlings in nature, and care must be exercised in the seasonal timing for planting young plants or cladodes of cultivated species to avoid stem overheating.

Water

Related to the tolerance by cacti of cellular desiccation during subzero episodes (Fig. 4.6) is the ability of cacti to withstand dehydration caused by drought. For *O. acanthocarpa, O. basilaris,* and *O. bigelovii,* uprooted plants can survive 3 years without water (Szarek and Ting 1975; Smith and Madhaven 1982). Moreover, *Copiapoa cinerea* can survive outdoors (Gulmon et al. 1979) and *Ferocactus wislizenii* indoors (MacDougal et al. 1915) for 6 years without water. *Carnegiea gigantea, F. acanthodes,* and *O. basilaris* can lose 80% of their stem water and still survive (Barcikowski and Nobel 1984), and *Coryphantha vivipara* can lose 91% of its stem water when exposed to drought and live (Nobel 1981). Indeed, the ability of cacti to tolerate cellular water loss, and hence drought, is correlated with their ability to tolerate intracellular water loss during subzero temperature episodes accompanied by extracellular ice formation.

Cacti can store an immense amount of water in their succulent stems. This has ramifications at the tissue level; during drought, water is shuttled from the internal whitish water-storage parenchyma to the greenish photosynthetic chlorenchyma, thereby allowing net CO_2 uptake to proceed for extended periods. For instance, the water-storage parenchyma in *Carnegiea gigantea* and *Ferocactus acanthodes* loses four times more water than does their chlorenchyma during drought (Barcikowski and Nobel 1984). Similar patterns of water loss are also exhibited by *O. basilaris* and *O. ficus-indica* (Barcikowski and Nobel 1984; Goldstein et al. 1991). Likewise, the water storage parenchyma loses more water than does the chlorenchyma in *O. humifusa* in response to cooling from day/night temperatures of 25°/15°C to 5°/−5°C (Loik and Nobel 1991).

Internal water redistribution reflects differences in the cellular properties of water-storage parenchyma and chlorenchyma. For *C. gigantea* and *F. acanthodes* exposed to drought, solutes are lost from the water storage parenchyma, thus creating a difference in the osmotic pressure between the two tissues and facilitating water movement into the chlorenchyma (Barcikowski and Nobel 1984). When *O. ficus-indica* is exposed to drought, the osmotic pressure in the water storage parenchyma becomes lower than in the chlorenchyma due to a polymerization of sugars leading to the formation of starch grains in the water-storage parenchyma (Goldstein et al. 1991). Water-storage parenchyma can also survive at a lower relative water content than chlorenchyma. Mucilage, which has a very high water-binding capacity, also occurs in greater amounts in the intercellular air spaces of water storage tissue than in the chlorenchyma (Goldstein et al. 1991). In addition, the elastic modulus of the cell walls of water storage parenchyma is only 40% of that of the chlorenchyma, allowing the water-storage parenchyma to maintain turgor over a large range of water contents.

Other aspects of water conservation and drought tolerance by cacti include relatively low stem stomatal frequencies of 20 to 80 per mm^2 compared with 100 to 300 per mm^2 for leaves of C_3 and C_4 species (Conde 1975;

Pimienta-Barrios et al. 1993; Nobel 1994). Therefore, only a small fraction of the surface area of cacti is available for water loss to the atmosphere. Also, the waxy cuticles covering the stems tend to be relatively thick for cacti—5 to 30 µm—compared with cuticles that are only 0.4 to 2 µm thick on the leaves of representative C_3 and C_4 species (Conde 1975; Pimienta-Barrios et al. 1993; North et al. 1995). As another adaptation, cacti have shallow roots, with a mean depth of only 10 to 15 cm, which facilitates responses to light rainfall; in addition, new roots develop rapidly once the soil is wet (Nobel 1988).

Salinity

Another factor that can be lethal for cacti is soil salinity. Indeed, cacti generally do not thrive in soils that are high in sodium chloride or calcium carbonate, which affects native populations and where opuntias can be cultivated. *Cereus validus* is native to the salt flats of Salinas Grandes, Argentina; this area experiences high salinity during the dry season, when its root system withers as water evaporates and salts collect near the soil surface (Nobel 1988). During the dry season, the sodium concentration increases in its roots and is progressively lower toward the apex of the stem (Nobel et al. 1984), as also occurs for *O. ficus-indica* (Berry and Nobel 1985). The increasing concentration of NaCl in the chlorenchyma of these two species as the soil salinity increases is accompanied by a decrease in net CO_2 uptake, as also occurs for *O. humifusa* (Silverman et al. 1988), and can eventually lead to plant death

Inhibition of growth for *O. ficus-indica* is approximately linear with soil sodium content, with 150 ppm by mass of Na leading to approximately 50% inhibition of shoot growth (Nobel 1989). A similar 50% inhibition of shoot growth can be caused by watering with 60 mM NaCl (12% of the salinity of seawater) for 6 months, which leads to 84% inhibition of root growth (Berry and Nobel 1985). Plant dry weight for *O. ficus-indica* is 60% less for plants irrigated with 200 mM NaCl compared with 5 mM NaCl (Nerd et al. 1991). Cladode water content is also 10% lower, and cladode osmotic pressure doubles for plants under the higher NaCl regime. For *Ferocactus acanthodes,* watering with 60 mM NaCl has relatively little effect on existing shoot biomass but reduces existing root biomass by 40% (Berry and Nobel 1985), again indicating that root growth is more sensitive to salinity than is shoot growth.

Gravity and Wind

Due to their mechanical strength, imparted primarily by the wood content in their stems (Gibson and Nobel 1986), cacti do not deflect greatly due to gravity or wind. The wood of the columnar cactus *Carnegiea gigantea* may get stiffer with plant age, making the stem resist deflection and buckling more per amount of wood area and allowing this species to reach heights of 15 m (Niklas and Buchman 1994). Also, stems of another columnar cactus, *Pachycereus pringlei,* are able to resist bending moments due to xylem accumulation being greater at the base of the plant, much in the same manner as typical dicotyledonous trees (Niklas et al. 1999). The ribs of this species also provide support, especially for young plants and younger tissue on older plants.

Branches of platyopuntias are able to resist applied forces with little deflection or deformation, even though the cladodes of a branch are connected by a junction that is usually small in cross-sectional area compared to the middle of the individual segments. For instance, for a cladode of *O. ficus-indica* that is 30 cm in length, the angular deflection of the junction with the underlying cladode, plus the cladode itself, is 6° when loaded by a force equal to the cladode mass perpendicular to the face of the cladode at the center of mass, 2° when the applied mass is parallel to the cladode's face, and 2° for a relatively high windspeed of 10 m s^{-1} (36 km $hour^{-1}$; Nobel and Meyer 1991). Thus, even though cladodes are thin compared with stems of many woody plants and the cladode junctions are relatively small in area compared with other regions of the branch, the shoots of *O. ficus-indica* are quite rigid.

For other cacti, stem failure under static or dynamic loading may actually be advantageous because it results in vegetative reproduction. It is believed that when the semierect shrub *Stenocereus gummosus* reaches its structural height limit, the failure of the stems leads to vegetative reproduction because the stems root after they come into contact with the ground, eventually forming dense colonies (Molina-Freaner et al. 1998). A hybrid platyopuntia in southern California also exhibits this type of vegetative reproduction (Bobich and Nobel 2001). In particular, the cladode junctions of the hybrid *O.* "*occidentalis*" are weaker than the junctions of either of its putative parent species, *O. ficus-indica* and *O. littoralis,* allowing *O.* "*occidentalis*" to form large thickets. These thickets are also large enough to survive fires that engulf isolated plants of *O. ficus-indica* and *O. littoralis,* thus giving *O.* "*occidentalis*" a selective advantage over its parent species in a chaparral region subject to periodic fires.

Conclusions and Future Prospects

Since the early research performed at the Desert Botanical Laboratory, information on the environmental biology of cacti has grown substantially. Interest in the physiology of

cacti is spurred by their extraordinary ability to survive high temperatures, high PPF, and especially drought. The utilization of CAM by most of the species in the family in coping with these environmental stresses has added to the interest in these plants and has led to investigations of net CO_2 uptake for species from all three subfamilies, as well as knowledge of water-use efficiency and productivity for select species. However, net CO_2 uptake and productivity have been investigated for only slightly more than 2% of the species in the family. Also, the environmental biology of cacti from certain regions, such as the Atacama Desert of Chile, is lacking, suggesting that much more field research is needed.

As ecological and agricultural interest in cacti grows, greater insight into their optimal growth conditions will become essential. This will require detailed analyses of the effects that temperature, light, and water have on CO_2 uptake for particular species. Greater attention should also be paid to how mineral nutrition affects net CO_2 uptake, because soil elements other than sodium have been studied only for their effects on nocturnal acid accumulation (Nobel 1983) or on productivity (Nobel et al. 1987; Nobel 1989). Moreover, the optimal soil properties, such as the sand, silt, and clay fractions, should be further investigated because some species have the ability to grow on various types of soil while others are restricted to special soil types (Benson 1982).

Although comparisons of net CO_2 uptake and productivity have been made between crops and certain cacti, particularly the highly productive *O. ficus-indica* (Nobel, 1988), comparisons of uncultivated cacti with sympatric species in their native habitat are rare. For example, *Opuntia humifusa* has received attention because it is the most widespread cactus in North America and is exposed to many different environmental stresses (Silverman et al. 1988; Loik and Nobel 1991). Yet, little is known about the net CO_2 uptake for *O. humifusa* compared to that of the many species with which it coexists or about which characteristics allow this species to compete successfully for resources in such a wide variety of habitats. Similarly, little is known about the productivity for most uncultivated epiphytic cacti, even though over 10% of the Cactaceae are epiphytes (Gibson and Nobel 1986). With the large amount of information on the utilization of CAM by other vascular epiphytes (Griffiths 1989; Zotz and Ziegler 1997), studies comparing their CO_2 uptake to that of epiphytic cacti in response to various environmental factors would aid in understanding the distribution and frequency of epiphytic cacti in the canopies of tropical forests.

New research possibilities for the environmental biology of cacti go far beyond the aforementioned topics. Improvements in instrumentation will facilitate investigations of the photosynthetic strategies for cacti and their ability to survive harsh conditions. Moreover, members of the Cactaceae occur natively from southern Argentina and Chile to Canada, and from coastal strand communities to tropical alpine environments, and are cultivated in more than 30 countries (Gibson and Nobel 1986; Nobel 1994). Almost endless possibilities exist for interesting environmental studies involving cacti.

Literature Cited

Adams, W. W., III, M. Diaz, and K. Winter. 1989. Diurnal changes in photochemical efficiency, the reduction state of Q, radiationless energy dissipation, and nonphotochemical fluorescence quenching in cacti exposed to natural sunlight in northern Venezuela. *Oecologia* 80: 553–561.

Barcikowski, W., and P. S. Nobel. 1984. Water relations of cacti during desiccation: distribution of water in tissues. *Botanical Gazette* 145: 110–115.

Barker, D. H., and W. W. Adams III. 1997. The xanthophyll cycle and energy dissipation in differently oriented faces of the cactus *Opuntia macrorhiza. Oecologia* 109: 353–361.

Benson, L. 1982. *The Cacti of the United States and Canada.* Stanford University Press, Stanford, California.

Berry, W. L., and P. S. Nobel. 1985. Influence of soil and mineral stresses on cacti. *Journal of Plant Nutrition* 8: 679–696.

Bobich, E. G., and P. S. Nobel. 2001. Biomechanics and anatomy of cladode junctions for two *Opuntia* (Cactaceae) species and their hybrid. *American Journal of Botany* 88: 391–400.

Cannon, W. A. 1925. *Physiological Features of Roots, with Especial Reference to the Relation of Roots to Aeration of the Soil.* Publication 368, Carnegie Institution of Washington, Washington, D.C.

Conde, L. F. 1975. Anatomical comparisons of five species of *Opuntia* (Cactaceae). *Annals of the Missouri Botanical Garden* 62: 425–473.

Cui, M., P. M. Miller, and P. S. Nobel. 1993. CO_2 exchange and growth of the Crassulacean acid metabolism plant *Opuntia ficus-indica* under elevated CO_2 in open-top chambers. *Plant Physiology* 103: 519–524.

Cui, M., and P. S. Nobel. 1994. Gas exchange and growth responses to elevated CO_2 and light levels for the

CAM species *Opuntia ficus-indica. Plant, Cell and Environment* 17: 935–944.

Drennan, P. M., and P. S. Nobel. 2000. Response of CAM species to increasing atmospheric CO_2 concentrations. *Plant, Cell and Environment* 23: 767–781.

Franco-Vizcaíno, E., G. Goldstein, and I. P. Ting. 1990. Comparative gas exchange of leaves and bark in three stem succulents of Baja California. *American Journal of Botany* 77: 1272–1278.

Garcia de Cortázar, V., and P. S. Nobel. 1991. Prediction and measurement of high annual productivity for *Opuntia ficus-indica. Agricultural and Forest Meteorology* 56: 261–272.

Garcia de Cortázar, V., and P. S. Nobel. 1992. Biomass and fruit production for the prickly pear cactus, *Opuntia ficus-indica. Journal of the American Society for Horticultural Science* 117: 558–562.

Garcia de Cortázar, V., E. Acevedo, and P. S. Nobel. 1985. Modeling of PAR interception and productivity by *Opuntia ficus-indica. Agricultural and Forest Meteorology* 34: 145–162.

Gerwick, B. C., and G. J. Williams III. 1978. Temperature and water relations of gas exchange of *Opuntia polyacantha. Oecologia* 35: 149–159.

Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer.* Harvard University Press, Cambridge, Massachusetts.

Goebel, K. 1895. Über die Einwirkung des Lichtes auf die Gestaltung der Kakteen und anderer Pflanzen. *Flora* 80: 96–116.

Goldstein, G., J. L. Andrade, and P. S. Nobel. 1991. Differences in water relations parameters for the chlorenchyma and the parenchyma of *Opuntia ficus-indica* under wet versus dry conditions. *Australian Journal of Plant Physiology* 18: 95–107.

Goldstein, G., and P. S. Nobel. 1994. Water relations and low-temperature acclimation for cactus species varying in freezing tolerance. *Plant Physiology* 104: 675–681.

Griffiths, D. 1915. *Yields of Native Prickly Pear in Southern Texas.* Bulletin 208, United States Department of Agriculture, Washington, D.C.

Griffiths, H. 1989. Carbon dioxide concentrating mechanisms and the evolution of CAM in vascular epiphytes. In *Vascular Plants as Epiphytes* (U. Lüttge, ed.). Springer-Verlag, Berlin. Pp. 42–81.

Gulmon, S. L., P. W. Rundel, and J. R. Ehleringer. 1979. Spatial relationships and competition in a Chilean desert cactus. *Oecologia* 44: 40–43.

Hanscom, Z., III, and I. P. Ting. 1978. Irrigation magnifies CAM-photosynthesis in *Opuntia basilaris* (Cactaceae). *Oecologia* 33: 1–15.

Hatzmann, S., G. Ebert, and P. Lüdders. 1991. Influence of NaCl salinity on growth, ion uptake, and gas exchange of *Opuntia ficus-indica* (L.) Miller. *Angewandte Botanik* 65: 161–168.

Inglese, P., A. A. Israel, and P. S. Nobel. 1994. Growth and CO_2 uptake for cladodes and fruit of the Crassulacean acid metabolism species *Opuntia ficus-indica* during fruit development. *Physiologia Plantarum* 91: 708–714.

Israel, A. A., and P. S. Nobel. 1995. Growth temperature versus CO_2 uptake, Rubisco and PEPCase activities, and enzyme high-temperature sensitivities for a CAM plant. *Plant Physiology and Biochemistry* 33: 345–351.

Kluge, M., and I. P. Ting. 1984. *Crassulacean Acid Metabolism: Analysis of an Ecological Adaptation.* Springer-Verlag, Berlin.

Koch, K. E., and R. A. Kennedy. 1980. Effects of seasonal changes in the Midwest on Crassulacean acid metabolism (CAM) in *Opuntia humifusa* Raf. *Oecologia* 45: 390–395.

Littlejohn, R. O., Jr. 1983. Environmental regulation of photosynthesis and characterization of phase II Crassulacean acid metabolism in three *Opuntia* species. Ph.D. Thesis, Washington State University, Pullman.

Loik, M. E., and P. S. Nobel. 1991. Water relations and mucopolysaccharide increases for a winter hardy cactus during acclimation to subzero temperatures. *Oecologia* 88: 340–346.

Loik, M. E., and P. S. Nobel. 1993. Freezing tolerance and water relations of *Opuntia fragilis* from Canada and the United States. *Ecology* 74: 1722–1732.

Long, E. R. 1915. Acid accumulation and destruction in large succulents. *The Plant World* 18: 261–272.

Luo, Y., and P. S. Nobel. 1993. Growth characteristics of newly initiated cladodes of *Opuntia ficus-indica* as affected by shading, drought, and elevated CO_2. *Physiologia Plantarum* 87: 467–474.

Lüttge, U., and P. S. Nobel. 1984. Day-night variations in malate concentration, osmotic pressure, and hydrostatic pressure in *Cereus validus. Plant Physiology* 75: 804–807.

MacDougal, D. T. 1924. *Growth in Trees and Massive Organs of Plants—Dendrographic Measurements.* Publication 350, Carnegie Institution of Washington, Washington, D.C.

MacDougal, D. T., and W. A. Cannon. 1910. *The Conditions of Parasitism in Plants.* Publication 129, Carnegie Institution of Washington, Washington, D.C.

MacDougal, D. T., E. R. Long, and J. G. Brown. 1915. End results of desiccation and respiration in succulent plants. *Physiological Researches* 1: 289–325.

MacDougal, D. T., and E. B. Working. 1922. A new high-temperature record for growth. *Carnegie Institution of Washington Year Book* 20: 47–48.

MacDougal, D. T., and E. B. Working. 1933. *The Pneumonic System of Plants, Especially Trees.* Publication 441, Carnegie Institution of Washington, Washington, D.C.

McGinnies, W. C. 1981. *Discovering the Desert: Legacy of the Carnegie Desert Botanical Laboratory.* University of Arizona Press, Tucson.

Mizrahi, Y., A. Nerd, and P. S. Nobel. 1997. Cacti as crops. *Horticultural Reviews* 18: 291–319.

Molina-Freaner, F., C. Tinoco-Ojanguren, and K. J. Niklas. 1998. Stem biomechanics of three columnar cacti from the Sonoran Desert. *American Journal of Botany* 85: 1082–1090.

Nerd, A., A. Karadi, and Y. Mizrahi. 1991. Salt tolerance of prickly pear cactus (*Opuntia ficus-indica*). *Plant and Soil* 137: 201–207.

Niklas, K. J., and S. L. Buchman. 1994. The allometry of saguaro height. *American Journal of Botany* 81: 1161–1168.

Niklas, K. J., F. Molina-Freaner, and C. Tinoco-Ojanguren. 1999. Biomechanics of the columnar cactus *Pachycereus pringlei. American Journal of Botany* 86: 767–775.

Nisbet, R. A., and D. T. Patten. 1974. Seasonal temperature acclimation of a prickly-pear cactus in south-central Arizona. *Oecologia* 15: 345–352.

Nobel, P. S. 1978. Surface temperatures of cacti—influences of environmental and morphological factors. *Ecology* 59: 986–996.

Nobel, P. S. 1980. Influences of minimum stem temperatures on ranges of cacti in southwestern United States and central Chile. *Oecologia* 47: 10–15.

Nobel, P. S. 1981. Influence of freezing temperatures on a cactus, *Coryphantha vivipara. Oecologia* 48: 194–198.

Nobel, P. S. 1982a. Low temperature tolerance and cold hardening of cacti. *Ecology* 63: 1650–1656.

Nobel, P. S. 1982b. Orientation, PAR interception, and nocturnal acidity increases for terminal cladodes of a widely cultivated cactus, *Opuntia ficus-indica. American Journal of Botany* 69: 1462–1469.

Nobel, P. S. 1982c. Orientations of terminal cladodes of platyopuntias. *Botanical Gazette* 143: 219–224.

Nobel, P. S. 1983. Nutrient levels in cacti—relation to nocturnal acid accumulation and growth. *American Journal of Botany* 70: 1244–1253.

Nobel, P. S. 1984. Productivity of *Agave deserti:* measurement by dry weight and monthly prediction using physiological responses to environmental parameters. *Oecologia* 64: 1–7.

Nobel, P. S. 1986. Relation between monthly growth of *Ferocactus acanthodes* and an environmental productivity index. *American Journal of Botany* 73: 541–547.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nobel, P. S. 1989. A nutrient index quantifying productivity of agaves and cacti. *Journal of Applied Ecology* 26: 635–645.

Nobel, P. S. 1991. Tansley Review No. 32. Achievable productivities of certain CAM plants: Basis for high values compared with C_3 and C_4 plants. *New Phytologist* 119: 183–205.

Nobel, P. S. 1994. *Remarkable Agaves and Cacti.* Oxford University Press, New York.

Nobel, P. S. 1996. Responses of some North American CAM plants to freezing temperatures and doubled CO_2 concentrations: Implications of global climate change for extending cultivation. *Journal of Arid Environments* 34: 187–196.

Nobel, P. S. 1999. *Physiochemical and Environmental Plant Physiology,* 2nd ed. Academic Press, San Diego, California.

Nobel, P. S., J. L. Andrade, N. Wang, and G. B. North. 1994. Water potentials for developing cladodes and fruits of a succulent plant, including xylem-versus-phloem implications for water movement. *Journal of Experimental Botany* 45: 1801–1807.

Nobel, P. S., and E. De la Barrera. 2000. Carbon and water balances for young fruits of platyopuntias. *Physiologia Plantarum* 109: 160–166.

Nobel, P. S., E. Garcia-Moya, and E. Quero. 1992. High annual productivity of certain agaves and cacti under cultivation. *Plant, Cell and Environment* 15: 329–335.

Nobel, P. S., G. N. Geller, S. C. Kee, and A. D. Zimmerman. 1986. Temperatures and thermal tolerances for

cacti exposed to high temperatures near the soil surface. *Plant, Cell and Environment* 9: 279–287.

Nobel, P. S., and T. L. Hartsock. 1983. Relationships between photosynthetically active radiation, nocturnal acid accumulation, and CO_2 uptake for a Crassulacean acid metabolism plant, *Opuntia ficus-indica. Plant Physiology* 71: 71–75.

Nobel, P. S., and T. L. Hartsock. 1984. Physiological responses of *Opuntia ficus-indica* to growth temperature. *Physiologia Plantarum* 60: 98–105.

Nobel, P. S., and T. L. Hartsock. 1986a. Leaf and stem CO_2 uptake in the three subfamilies of the Cactaceae. *Plant Physiology* 80: 913–917.

Nobel, P. S., and T. L. Hartsock. 1986b. Environmental influences on the productivity of three desert succulents in the south-western United States. *Plant, Cell and Environment* 9: 741–749.

Nobel, P. S., and T. L. Hartsock. 1986c. Short-term and long-term responses of Crassulacean acid metabolism plants to elevated CO_2. *Plant Physiology* 82: 604–606.

Nobel, P. S., and T. L. Hartsock. 1987. Drought-induced shifts in daily CO_2 uptake patterns for leafy cacti. *Physiologia Plantarum* 70: 114–118.

Nobel, P. S., and T. L. Hartsock. 1990. Diel patterns of CO_2 exchange for epiphytic cacti differing in succulence. *Physiologia Plantarum* 78: 628–634.

Nobel, P. S., and A. A. Israel. 1994. Cladode development, environmental responses of CO_2 uptake, and productivity for *Opuntia ficus-indica* under elevated CO_2. *Journal of Experimental Botany* 45: 295–303.

Nobel, P. S., and M. E. Loik. 1990. Thermal analysis, cell viability, and CO_2 uptake of a widely distributed North American cactus, *Opuntia humifusa,* at subzero temperatures. *Plant Physiology and Biochemistry* 28: 429–436.

Nobel, P. S., M. E. Loik, and R. W. Meyer. 1991. Microhabitat and diel tissue acidity changes for two sympatric cactus species differing in growth habit. *Journal of Ecology* 79: 167–182.

Nobel, P. S., U. Lüttge, S. Heuer, and E. Ball. 1984. Influence of applied NaCl on Crassulacean acid metabolism and ionic levels in a cactus, *Cereus validus. Plant Physiology* 75: 799–803.

Nobel, P. S., and R. W. Meyer. 1991. Biomechanics of cladodes and cladode-cladode junctions for *Opuntia ficus-indica* (Cactaceae). *American Journal of Botany* 78: 1252–1259.

Nobel, P. S., and E. Pimienta-Barrios. 1995. Monthly stem elongation for *Stenocereus queretaroensis:* Relationships to environmental conditions, net CO_2 uptake and seasonal variations in sugar content. *Environmental and Experimental Botany* 35: 17–24.

Nobel, P. S., C. E. Russell, P. Felker, J. G. Medina, and E. Acuña. 1987. Nutrient relations and productivity of prickly pear cacti. *Agronomy Journal* 79: 550–555.

Nobel, P. S., N. Wang, R. A. Balsamo, M. E. Loik, and M. A. Hawke. 1995. Low-temperature tolerance and acclimation of *Opuntia* spp. after injection of glucose or methylglucose. *International Journal of Plant Sciences* 156: 496–504.

North, G. B., T. L. Moore, and P. S. Nobel. 1995. Cladode development for *Opuntia ficus-indica* (Cactaceae) under current and doubled CO_2 concentrations. *American Journal of Botany* 82: 159–166.

Osmond, C. B. 1978. Crassulacean acid metabolism: A curiosity in context. *Annual Review of Plant Physiology* 29: 379–414.

Osmond, C. B., M. M. Ludlow, R. Davis, I. R. Cowan, S. B. Powles, and K. Winter. 1979. Stomatal responses to humidity in *Opuntia inermis* in relation to control of CO_2 and H_2O exchange patterns. *Oecologia* 41: 65–76.

Pimienta-Barrios, E., M. Luera-Quezada, and L. L. Lopez Amezcua. 1993. Estudio anatómico comparativo en colectas del subgenero Opuntia. *Agrociencia, Series Fitociencia* 4: 7–14.

Pimienta-Barrios, E., and P. S. Nobel. 1998. Vegetative, reproductive, and physiological adaptations to aridity of pitayo (*Stenocereus queretaroensis,* Cactaceae). *Economic Botany* 52: 401–411.

Raveh, E., M. Gersani, and P. S. Nobel. 1995. CO_2 uptake and fluorescence responses for a shade-tolerant cactus *Hylocereus undatus* under current and doubled CO_2 concentrations. *Physiologia Plantarum* 93: 505–511.

Richards, H. M. 1915. *Acidity and Gas Interchange in Cacti.* Publication 209, Carnegie Institution of Washington, Washington, D.C.

Russell, C. E. and P. Felker. 1987. Comparative cold hardiness of *Opuntia* spp. and cvs. grown for fruit, vegetable, and fodder production. *Journal of Horticultural Science* 2: 545–550.

Shreve, F. 1931. *The Cactus and Its Home.* Williams and Wilkins, Baltimore.

Silverman, F. P., D. R. Young, and P. S. Nobel. 1988.

Effects of applied NaCl on *Opuntia humifusa. Physiologia Plantarum* 72: 343–348.

Smith, B. N., and S. Madhaven. 1982. Carbon isotope ratios in obligate and facultative CAM plants. In *Crassulacean Acid Metabolism* (I. P. Ting and M. Gibbs, eds.). American Society of Plant Physiologists, Rockville, Maryland. Pp. 231–243.

Smith, S. D., B. Didden-Zopfy, and P. S. Nobel. 1984. High-temperature responses of North American cacti. *Ecology* 65: 643–651.

Szarek, S. R., and I. P. Ting. 1975. Photosynthetic efficiency of CAM plants in relation to C_3 and C_4 plants. In *Environmental and Biological Control of Photosynthesis* (R. Marcelle, ed.). Dr. W. Junk, The Hague. Pp. 289–297.

Taiz, L., and E. Zeiger. 1998. *Plant Physiology,* 2nd ed. Sinauer Associates, Sunderland, Massachusetts.

Turnage, W. V., and A. L. Hinckley. 1938. Freezing weather in relation to plant distribution in the Sonoran Desert. *Ecological Monographs* 8: 529–550.

Troughton, J. H., P. V. Wells, and H. A. Mooney. 1974. Photosynthetic mechanisms in ancient C_4 and CAM species. *Carnegie Institution Year Book* 73: 812–816.

Uphof, J. C. Th. 1916. *Cold-Resistance in Spineless Cacti.* Bulletin 79, University of Arizona Agricultural Experiment Station, Tucson.

Wang, N., and P. S. Nobel. 1995. Phloem exudate collected via scale insect stylets for the CAM species *Opuntia ficus-indica* under current and doubled CO_2 concentrations. *Annals of Botany* 75: 525–532.

Wang, N., H. Zhang, and P. S. Nobel. 1997. Phloem-xylem water flow in developing cladodes of *Opuntia ficus-indica* during sink-to-source transition. *Journal of Experimental Botany* 48: 675–682.

Zotz, G., and H. Ziegler. 1997. The occurrence of Crassulacean acid metabolism among vascular epiphytes from Central Panama. *New Phytologist* 137: 223–229.

CHAPTER

› 5 ‹

REPRODUCTIVE BIOLOGY

Eulogio Pimienta-Barrios and Rafael F. del Castillo

Introduction
Areoles and Reproductive Structures
Flower Types, Pollinators, and Pollination
Outcrossing Mechanisms
Polyploidy and Reproduction
Flower Fertilization
Flower and Fruit Development
Seed Germination
Apomixis
Conclusions
Literature Cited

Introduction

Cacti are native to the Americas, where they are widely distributed. More than 70% of the species occur in arid and semiarid regions of Mexico, Peru, Argentina, and Chile (Gibson and Nobel 1986; Arias-Moreno 1997). Water is the major limiting factor for plant productivity in such environments (Fischer and Turner 1978), although other factors, such as strong drying winds, extreme temperatures, limited nutrients, and high light intensity, can exacerbate the effects of water scarcity (Berry et al. 1983). Cacti perhaps provide the best examples of adaptations to aridity, including morphological modifications (e.g., succulence, low stomatal density, thick cuticles) and Crassulacean acid metabolism (Gibson and Nobel 1986; Nobel 1995). However, with the exception of seed germination and establishment (Rójas-Aréchiga and Vázquez-Yanes 2000), the role of most of the reproductive adaptations of cacti to aridity has been poorly studied and comes mainly from experiments with cultivated plants (Pimienta-Barrios and Nobel 1998). Nevertheless, studies on reproductive development for cacti in arid environments can help explain the evolution of reproductive mechanisms in cacti, which allow them to cope with the prevailing physical and chemical stresses. This review describes the available information on reproductive biology, relating various aspects to the adaptations of cacti to aridity and to the origin and causes of biological variation.

Areoles and Reproductive Structures

The distinctive vegetative structure of cacti is the areole, considered homologous to a lateral (axillary) bud (Buxbaum 1950). Hairs, foliar organs, reproductive organs, glochids, and roots develop from the areoles (Booke 1980). Cactus flowers are sessile and solitary, and commonly only one flower is produced per areole, which helps increase fruit set for cacti (Ramírez and Berry 1995). However, several flowers are sometimes derived from a single areole,

e.g., for *Pterocereus foetidus* (Bravo-Hollis 1978). For *Myrtillocactus,* several areoles join to produce an inflorescence in which the flowers appear to be derived from a single meristem (Buxbaum 1950). For *Opuntia prolifera,* a chain of fruits results from the development of flowering buds derived from pericarpic areoles. The flowers are usually campanulate with radial symmetry (actinomorphic), but in epiphytic species the flowers are lightly bilateral (zygomorphic), as the stamens and styles are located in the ventral part of the flower (Arreola-Nava 1997). The large, attractive flowers for which cacti are noted occur in most self-fertile polyploids (Ross 1981). For instance, the flowers of *Opuntia* are large, and mature flowers can vary from 6 to 10 cm in length; they commonly are borne near the apex of the cladodes (Gibson and Nobel 1986). The flowers of *Cereus peruvianus, Hylocereus* spp., and *Selenicereus megalanthus* are among the largest in the cactus family (Nerd and Mizrahi 1997).

Cactus flowers usually open and close during the same day. For opuntias (Fig. 5.1), flower opening typically lasts 8 to 11 hours (Rosas and Pimienta 1986; del Castillo and González-Espinosa 1988; Osborn et al. 1988; Mandujano et al. 1996), but some flowers may open a second day (Grant and Grant 1981; Rosas and Pimienta 1986). Ephemeral flowers are common in dry tropical rainforests; this flower behavior apparently decreases water loss by decreasing the time available for transpiration (Primack 1982).

The most fundamental characteristic of a cactus flower is its inferior ovary, meaning that the ovary occurs below the perianth parts and the stamens (Fig. 5.2); only a few *Pereskia* spp. have superior ovaries (Bravo-Hollis 1978; Gibson and Nobel 1986). Cacti are among the few plants in which the exterior of an inferior ovary is sunken into a modified stem, termed the receptacle (Booke 1980). The ovary is formed by the fusion of several carpels and consists of a single internal chamber, the locule, where a relatively high number of ovules occur in a parietal location along the ventral wall of the ovary (Fig. 5.2; Booke 1980). The number of ovules per flower is 150 to 400 for *Opuntia ficus-indica* (Rosas and Pimienta 1986; Weiss et al. 1993), 388 (hermaphrodites) to 406 (females) for *O. robusta* (del Castillo 1986a), over 1,000 for *Stenocereus queretaroensis* (Pimienta-Barrios and Nobel 1995), and 7,200 for *Hylocereus undatus* (Nerd and Mizrahi 1997).

A unique type of ovule is found in the Cactaceae. Due to unilateral growth, it first becomes anatropous and, as the curvature continues, the micropyle again points upward in the fully formed ovule (Bhojwani and Bhatnagar 1979). Embryological observations for *Opuntia* and *Stenocereus* spp. (Rosas and Pimienta 1986; Ortega, 1993; García-Aguilar and Pimienta-Barrios 1996) reveal that most of the embryological characters are primitive, according to Grayum's (1991) criteria. The embryological characters are: (1) the inferior position of the ovary, (2) four microsporangia per anther, (3) isobilateral type of microspore tetrads, (4) bitegmic and crassinucelated ovules, (5) the functional megaspore in the chalazal position, (6) embryo of the polygon type, (7) the high number of ovules per ovary, and (8) glandular tapetal tissue (Grayum 1991; Ortega 1993).



Figure 5.1. *Opuntia* flower at the initial stages of opening, when only the basal part of the stigma is covered with pollen grains released before opening from anthers in contact with the basal part of the stigmatic surface.

The style can be short and thick, as for *Opuntia* spp., or long and thin, as for *Heliocereus* spp. (Arreola-Nava 1997). The stigma is at the apex of the style (Fig. 5.2), where pollen is deposited, and shows a variable number of lobes—from 3, as for *Mammillaria,* to 24 for *Hylocereus* (Arreola-Nava 1997). The stigma of most cactus flowers shows characteristics suitable for insect landing, because it is over the stamens (Grant and Grant 1979b; Ross 1981; del Castillo and González-Espinosa 1988). Both the large stigmatic surface and the stickiness of the receptive surface improve the chances of catching pollen grains. The nectary usually lies at the base of the thickened style, forming a chamber at the base of the receptacle, where substantial nectar accumulates. Nectar can be rich in sucrose, as for *Pachycereus pringlei* (Fleming et al. 1994), and is usually secreted at the beginning of anthesis (del Castillo and González-Espinosa 1988; Mandujano et al. 1996). In the Peruvian genus *Matucana,* the nectar chamber is closed by a protective device that probably prevents dilution of the nectar (Bregman 1996).

The numerous stamens of a cactus flower are spirally arranged and have thigmotropic sensitivity; i.e., they move

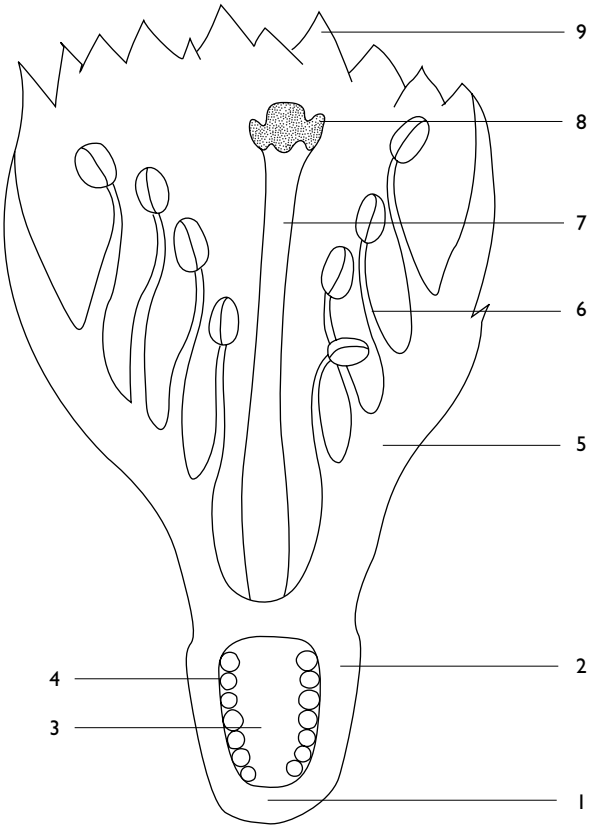


Figure 5.2. Longitudinal section of a *Mammillaria* flower: (1) peduncular zone; (2) receptacular tissue; (3) locular cavity; (4) ovules in a parietal position; (5) receptacular tube; (6) stamen; (7) style; (8) stigmatic lobule; and (9) perianth segment. Modified from Bravo-Hollis (1978).

when touched (Rosa and Pimienta 1986). The thigmotropic movements can facilitate pollen collection by insects during floral visits (Grant and Hurd 1979) and also promote self-pollination (Rosas and Pimienta 1986). The number of pollen grains produced per flower varies from 160,000 for *O. rastrera* (Mandujano et al. 1996) to 330,000 for *O. robusta* male plants (del Castillo 1986a). The number of ovules per flower for opuntias varies from 150 to 400 (Rosas and Pimienta 1986; Nerd and Mizrahi 1997), so the number of pollen grains per ovule varies from 400 to 800. The ratio is low compared with that for anemophilous (wind pollinated) flowers producing 500,000 to 3,000,000 pollen grains per ovule, and from 5,000 to 100,000 pollen grains per ovule for entomophilous (insect pollinated) plants (Linskens 1983). Similarly low pollen grains-to-ovule ratios occur for five species of Venezuelan columnar cacti: *Pilosocereus moritzians, P. lanuginosus, Stenocereus griseus, Subpilocereus horispinus,* and *S. repandus*—300 to 1,050 (Nassar et al. 1997). Low investment of energy in the production of male gametophytes may be a strategy to save energy in stressful environments.

Flower Types, Pollinators, and Pollination

Studies on cactus pollination span more than a century (Toumey 1895; Mandujano et al. 1996), although many genera of cacti have not been studied at all. The pollination vectors for cacti are animals that exhibit specificity but not exclusivity. Based on the main pollinators attracted, cactus flowers can be roughly classified as bee flowers, moth flowers, hummingbird flowers, and bat flowers (Porsch 1938, 1939; Grant and Grant 1979c).

The typical bee flower is bowl- or cup-shaped (Fig. 5.1) and has many perianth segments, a brightly color perianth, diurnal periodicity, numerous stamens, a single style, and a lobed stigma (Grant and Hurd 1979; del Castillo and González-Espinosa 1988; del Castillo 1994, 1999). The perianth is usually yellow, but may be pinkish, orange, magenta, red, or violet. The color may turn darker after the flowers are pollinated, as for some opuntias. Red or other colored stripes are present in some species of *Ferocactus, Mammillaria,* and *Stenocactus.* Ultraviolet floral patterns may increase pollinator visits and efficiency, as observed for *Echinocereus* spp. (Leuck and Miller 1982).

Although butterflies, diptera, beetles, and hummingbirds are also flower visitors, bees are the most frequent and the most likely pollinators. Nearly 20 genera of native bees as well as the common honey bee, *Apis mellifera,* are flower visitors, but not all of them are equally efficient for pollination. Various factors apparently determine the effectiveness for bee pollination of cacti: (1) flying activity, (2) flower size, (3) constancy, and (4) the adherence of pollen grains to the body. Large bees, such as bumblebees (*Bombus* spp., 11–19 mm in body length), may be important pollinators because, although they are generalists, they perform long-distance flights that favor outcrossing between distant individuals. Medium-sized bees, such as *Diadasia* spp. (10–14 mm in body length), are the major pollinators of several species whose flowers are 50 to 70 mm in perianth diameter, such as many *Opuntia* spp. (Fig. 5.1; Grant and Hurd 1979; del Castillo and González-Espinosa 1988) and *Echinocereus* spp. (Grant and Grant 1979a; Leuck and Miller 1982). They have good pollen adherence to their bodies, are very active flying among the flowers, and are the most common floral visitors for these species. They usually land on the stigma, where the pollen is deposited, and then submerge into mass of stamens to visit the nectary and collect nectar.

Bee pollinators select whether or not to visit a cactus flower based on floral size. For bee-pollinated species with

a small floral diameter (40–45 mm), such as *Ferocactus histrix* and *Diadasia* spp., medium-sized bees are less-frequent visitors. Instead, smaller bees (e.g., *Ashmeadiella* spp., 5–7 mm in body length) are the major pollinators (del Castillo 1994). These bees also are less common flower visitors for opuntias and, because of their small size, when they do enter flowers, they may do so without touching the stigma (del Castillo and González-Espinosa 1988). Cacti with small, bowl-shaped flowers, such as *Epithelantha* spp., are probably mostly autogamous and depend little on pollinators to set seed (Grant and Grant 1979c). Small bees visit the small, bowl-shaped flowers of *Mammillaria* spp. Pollinators are needed even for certain self-compatible species to set seed, such as *O. lindheimeri* (Grant et al. 1979). Usually nectar is the main reward for bees. Some species, however, do not produce nectar, e.g., *O. lindheimeri* (Grant et al. 1979). Because this species coexists with nectar-producing opuntias with the same floral design, this may be considered an example of Batesian mimicry for cacti (Roy and Widmer 1999). It may also be an adaptation for moisture conservation (Grant and Hurd 1979).

The number of cacti that produce bee flowers suggests that this flower type is the most successful, or at least most common where cacti evolved. Perhaps its major disadvantage lies in the promiscuity of the pollinators, which may be a problem in areas rich in cactus diversity, where pollination among different species or genera is common (Leuck and Miller 1982; Grant and Hurd 1979; García-Sánchez 1984; del Castillo 1994). Promiscuity enhances hybridization and probably promotes evolutionary changes of the breeding system or the pollinator syndromes. A filter that maintains the individuality is the specificity of the pollination mechanisms (Linskens 1983).

Typical hummingbird flowers are red, diurnal, tubular, and zygomorphic. The stamens usually rise well above the tepals. Interestingly, this floral syndrome is more common in epiphytic cacti from humid habitats, such as cloud forests, than other cactus habitats. Many epiphytic species of *Schlumbergera* (McMillan and Horobin 1995), *Disocactus,* and *Nopalxochia* also have this floral syndrome. *Opuntia* spp. seems to have an interesting evolutionary transition from a bee-pollinated syndrome to the hummingbird syndrome. Some species have color variations that diverge from the typical yellow flower of many bee-pollinated cacti to red, while preserving the same floral shape (Arias-Moreno and Arreola-Nava 1995). The flowers of *O. stenopetala* are red, have a closed perianth, are nearly tubular, and are attractive to hummingbirds. *Nopalea,* which is closely related to *Opuntia,* has a typical hummingbird flower and is commonly visited and probably pollinated by these birds. In addition, the South American genus *Tacinga,* which is intermediate between *Nopalea* and *Opuntia,* has flowers with erect and non-sensitive stamens (typical of *Nopalea*) and narrow, green, recurved petals (Britton and Rose 1937).

Pollination by bats occurs for columnar cacti, such as *Carnegia gigantea* (Alcorn et al. 1961), *Neobuxbaumia* spp. (Valiente-Banuet et al. 1997), *Pachycereus pringlei* (Fleming et al. 1994), *Pilosocereus* spp. (Zappi 1994), *Stenocereus pruinosus* (Valiente-Banuet et al. 1997), and *S. stellatus* (Ramírez-Mireles 1999). Bat-pollinated flowers are usually large, robust, nocturnal, white or cream, and odoriferous, and produce abundant nectar. The flowers of columnar cacti attract bees and hummingbirds during the daytime and moths during nighttime (Valiente-Banuet et al. 1997). *Leptonycteris* spp. are common pollinators of cacti with bat-attracting flowers, and they may consume the pollen (Alcorn et al. 1961). Symbiosis with bats has at least three advantages for cacti: (1) lower promiscuity compared to bee flowers, (2) long distance flying (Fleming et al. 1994), and (3) seed dispersal by the bats (Fleming et al. 1994; Valiente-Banuet et al. 1997).

Moths commonly visit large, nocturnal, white, disc-shaped flowers, which are partially zygomorphic (most of the stamens lie on one side of the flower) and have a large nectarial chamber. Many genera of epiphytic cacti, such as *Hylocereus* (Ramírez-Mireles 1999), *Echinopsis, Epiphylum,* and *Selenicereus* (Rowley 1980), bear these flowers. Flowers of *Hylocereus* open at dusk but may remain open until the next morning, when they are visited by bees and bumblebees, which appear to be the major pollinators (Ortíz-Hernández 1999; Ramírez-Mireles 1999). Nectar is a major reward for moths. In their attempt to reach the nectary, moths visiting flowers of *Hylocereus* leave many of their wing scales on the style, darkly staining it and thus providing an easy means for detecting moth visits (Y. Ortíz-Hernández, personal communication). Some cylindropuntias have nocturnal disc-shaped flowers, instead of the typical diurnal bowl-shaped flowers (Grant and Hurd 1979).

Whereas bees, bats, hummingbirds, and moths are attracted by cactus flowers and pollinate them, the role of other flower visitors, such as beetles, ants, and birds other than hummingbirds, is not well established. Beetles commonly visit flowers of many species of cacti, such as those with bowl-shaped flowers (e.g., *Echinocereus, Ferocactus, Echinocactus, Mammillaria,* and *Opuntia;* Grant and Connell 1979; Grant and Grant 1979a; Grant and Hurd 1979; García-Sánchez 1984; del Castillo and González-

Espinosa 1988; del Castillo 1994). However, they are not good pollinators, as few pollen grains adhere to their bodies. Also, some beetles stay in a single flower, chewing floral parts. In fact, beetles in the genera *Camptodes, Carpophilus,* and *Trichochrous* invade the flowers in large groups and perform few flights among them (Grant and Connell 1979; Grant and Hurd 1979; García-Sánchez 1984; del Castillo and González-Espinosa 1988; del Castillo 1994). These beetles may self-pollinate the flowers directly or by stimulating thigmotrophic movements of the stamens, favoring the deposition of self-pollen on the stigma. In most cases, however, beetles may be nectar and pollen thieves. For *Pilosocereus,* a columnar cactus pollinated by bats, small beetles lay eggs in the flowers. The emerging larvae perforate the ovary and the stem (Zappi 1994).

Carnegiea gigantea in the Sonoran Desert can be pollinated by western white-winged doves, although they are not the main pollinator (Alcorn et al. 1961). In the Galápagos Islands, finches are common visitors of *Opuntia echios* and *O. helleri,* from which they remove the stigma to gain access to pollen and the nectar. In getting a short-term benefit, they potentially suffer in the long term through a diminished supply of seeds, which they also eat during the dry season (Grant and Grant 1981). Ants also visit cactus flowers. They may be attracted by the extrafloral nectaries, a modified spine that secretes nectar in various genera, such as *Coryphantha, Ferocactus,* and *Opuntia.* Nectar production usually coincides with flowering or fruiting. Ants do not pollinate the flowers, but they may help protect the plant from potential herbivores. For *Ferocactus histrix,* territorial and entomophagous ants (genera *Dorymyrmex* and *Iridomyrmex*) consume the nectar of extrafloral nectaries. They may even build their nests on top of the plants (del Castillo 1988a). For *O. acanthocarpa,* ants attracted by the extrafloral nectaries may increase fruit set and decrease fruit abortion by reducing the herbivore activity of coreid (Hemiptera: Coreidae) bugs (Pickett and Clark, 1979).

Outcrossing Mechanisms

Outcrossing is common among cacti. Of the 55 taxa studied by Ross (1981), seeds are produced upon self-pollination in only 11 taxa and by cross-pollination in the other 44 taxa. Cacti have several adaptations favoring outcrossing: self-incompatibility, dichogamy, herkogamy, and unisexuality. Incompatibility is a genetic barrier in the progamic phase that may take place between pollen and stigma or during the development of pollen tubes in the style. The latter occurs for some *Opuntia* spp. (Bullock 1985; Rosas 1984; Negrón-Ortiz 1998), for varieties of *Hylocereus* spp. (Ramírez-Mireles 1999), and for *Schlumbergera* (McMillan and Horobin 1995). The inhibition of the pollen tube in the style, after it has penetrated the stigma, is a characteristic of the gametophytic system of incompatibility (Lewis 1979; de Nettancourt 1997). But cacti do not share all of the characteristics typical of this incompatibility mechanism. For instance, the pollen in cacti is tri-nucleate (Benson 1979), whereas pollen in the typical gametophytic system is bi-nucleate (de Nettancourt 1997).

Other examples of obligate outcrossing cacti are *Carnegia gigantea* (Alcorn et al. 1961), *Ferocactus histrix, Nopalea auberi* (R. del Castillo, personal observations), *Neobuxbaumia* spp. (Valiente-Banuet et al. 1997), *Opuntia helleri,* and *O. echios* (Grant and Grant 1981). Self-incompatibility also occurs for *Astrophytum, Pediocactus, Stenocereus griseus, S. repandus, S. horrispinus,* and *Thelocactus* (Nassar et al. 1997) and in clones of *Cereus peruvianus, Hylocereus costaricensis,* and *H. polyrhizus* (Weiss et al. 1994a,b, 1995). For *O. leucotricha,* both selfing and interspecific hybrid crosses lead to low rates of fruit and seed set relative to outcrossing (Trujillo and González-Espinosa 1991).

In several hermaphroditic species of cacti, male and female organs mature at different times inside the flower. This phenomenon, called dichogamy, may reduce self-fertilization. For instance, in *Hylocereus* spp. cultivars, the stigma becomes receptive about 3 hours after the anthers dehisce (Ramírez-Mireles 1999), and pollen germinability is highest at anthesis. For *F. histrix,* pollen is released 1 to 2 days after anthesis. At this stage, the stigma lobes are closed, and the pollinators usually land directly on the stamens to reach the nectary. In this way, pollen can be easily collected. After 2 to 3 days of opening, the stigma lobes expand and are used by pollinators as a landing platform, and pollen from others flowers can be deposited (del Castillo 1994). Therefore, selfing within the same flower is avoided but the transfer of pollen from one flower to another in the same plant (geitonogamy) is not, as flowering is sequential.

Whereas dichogamy implies a temporal separation in the maturation of male and female flower parts, herkogamy is the spatial separation of anthers and stigma. The degree to which the stigmatic area is in contact with the anthers influences the probability of selfing. Grains of self pollen can occur on the lower portions of the stigma, which is in contact with the anthers, whereas outcross pollen is deposited on the upper surface of the stigma, as seen in a cultivar of *O. ficus-indica* (Fig. 5.1; Rosas and Pimienta 1986). Moreover, the fraction of the stigmatic surface in contact with the anthers is positively correlated with

the rate of autogamy for *Opuntia* (Trujillo and González-Espinosa 1991). For *Hylocereus undatus,* the distance between the stigma and anthers is large, thus decreasing the probability of autogamy (Y. Ortíz-Hernández, personal communication). This distance—and thus the probability of outcrossing—can change during the flowering season (Grant et al. 1979). The distance between the style and the stigma of *Nopalea* spp. changes during flower maturation. During opening when the pollen is released, the distance is less, increasing later when the stigma becomes receptive.

While most cacti are hermaphroditic, interesting exceptions occur for *Echinocereus, Mammillaria, Neobuxbaumia, Opuntia, Pachycereus,* and *Selenicereus* (del Castillo 1986a; Fleming et al. 1994; Valiente-Banuet et al. 1997). Atrophied organs of the non-functional sex and close hermaphroditic relatives of unisexual individuals suggest that unisexuality is a derived condition for cacti, as for other flowering plants. Unisexuality appears to have evolved several times independently. Dioecious populations (a population containing both male and female individuals) have been detected in *Echinocereus coccineus, Opuntia robusta,* and *O. stenopetala* (del Castillo and González-Espinosa 1988; Fleming et al. 1998). Trioecy (male, female, and hermaphroditic individuals in a single population) is reported for *O. robusta* and *Pachycereus pringlei* (del Castillo and González-Espinosa 1988; Fleming et al. 1998), gynodioecy (female and hermaphroditic individuals) for *P. pringlei* (Fleming et al. 1998), and androdioecy (male and hermaphroditic individuals in the same population) for *Neobuxbaumia mezcalaensis* (Valiente-Banuet et al. 1997).

Polyploidy and Reproduction

Cacti have a great range of polyploidy (Pinkava et al. 1977, 1985; Cota and Philbrick 1994). The significance of polyploidy, however, has not been related to the biology of the plants, particularly the mode of reproduction (Ross 1981). Changes in polyploidy can modify the breeding system of plants by at least two mechanisms: (1) by modifying the magnitude of inbreeding depression, and (2) by breaking down incompatibility mechanisms. Some species of cacti that have low rates of inbreeding depression are tetraploids —e.g., *O. robusta* (Sosa and Acosta 1966) and *Pachycereus pringlei* (Fleming et al. 1994). Ross (1981) reviewed 55 taxa of cacti and noted that polyploidy is correlated with self-fertility. In other families, chromosome doubling breaks down incompatibility mechanisms (Lewis 1979). Differences in inbreeding depression among diploids and polyploids probably have large influences on the evolution of polyploidy and breeding systems of cacti. Triploidy and tetraploidy most likely originated from fertilization involving gametes that had not undergone a reduction in their chromosome number (Lewis 1980), and fertilization of unreduced gametes accounts for several intraspecific polyploid *Opuntia* hybrids (Pinkava et al. 1985). A comparison of the ploidy level with the mode of reproduction in the Cactaceae suggests that polyploidy is more likely to become established in self-fertile or apomictic (producing seeds in the absence of fertilization) taxa (Ross 1981).

Flower Fertilization

The processes that occur from the arrival of pollen grain deposition onto the stigma to when the sperm reach the egg cell have received little attention (Rójas-Aréchiga and Vázquez-Yanes 2000). For the progamic phase of *Opuntia ficus-indica,* anther dehiscence occurs just before or at the time of flower opening, so pollen grains can start germination on the stigmas a few hours before the flowers open (Rosas 1984). Each stigma receives many pollen grains, but only a few germinate (about 30%; Weiss et al. 1993). Consequently, relatively few pollen tubes grow in the upper part of the style—from 300 to 350 per flower (Table 5.1). Pollen grain germination and pollen tube growth occur relatively rapidly, with over 20 pollen tubes occurring at the base of the style within 24 hours after flower opening, increasing to 65 tubes by 48 hours after flower opening. By the time the style wilts (72 hours after pollination), the number of pollen tubes at the base of the style exceeds 100 (Table 5.1).

Ovule fertilization is porogamous for both *Opuntia* and *Stenocereus,* because the pollen tubes penetrate the ovule through the micropyle before reaching the embryo sac (Rosas and Pimienta 1986; Ortega 1993). The first ovules with signs of fertilization occur 2 days after flower opening for *Opuntia.* At this time, the percentage of fecund ovules is low (2%), reaching 46% 2 days later. Because of the high number of ovules per flower (over 250), the ovule fertilization continues until 10 days after pollination. Ovule viability is high, because the percentage of ovules that are fertilized and transformed in seeds is high (over 80%; Rosas and Pimienta 1986).

Flower and Fruit Development

Early ontogeny of cactus flowers, including the initiation of floral organs, is similar to that in many other species. In the Northern Hemisphere, flower bud differentiation for most cacti begins at the end of winter and the beginning of spring; anthesis begins in the spring followed by the development of fruit, which mature during the summer, e.g., for *Opuntia* spp. (Bravo-Hollis 1978; Trujillo 1982; del Castillo and González-Espinosa 1988; Pimienta-Barrios 1990;

TABLE 5.1
Position and frequency of pollen tubes at different times after natural pollination for flowers of *Opuntia ficus-indica*

Hours after pollination	Number of pollen tubes at different positions along style			
	Stigma–¼	*¼–½*	*½–¾*	*¾–base of style*
24	344 ± 49	192 ± 10	63 ± 29	21 ± 4
48	355 ± 41	220 ± 25	126 ± 35	65 ± 9
72	325 ± 26	225 ± 26	151 ± 20	102 ± 31

Data are means ± SE (n = 10 styles). Adapted from Rosas and Pimienta (1986).

Mandujano et al. 1996). For *Echinocactus, Ferocactus, Myrtillocactus, Pachycereus,* and *Stenocereus,* flower differentiation and fruit development start earlier, and fruit ripening occurs at the end of the spring (Trujillo 1982; Gibson and Nobel 1986; del Castillo 1988a; Pimienta-Barrios 1999).

Another common reproductive feature of cacti is that flower development is asynchronous. Namely, flowers in early stages of differentiation, flowers at anthesis, and young developing fruits can occur simultaneously (Fig. 5.3; Trujillo 1982; del Castillo 1988a; Pimienta-Barrios 1990; Lomelí and Pimienta 1993). The asynchronous patterns of flower and fruit production may be especially advantageous during adverse environmental conditions (Pimienta-Barrios and Nobel 1995). Also, some cacti may have a second blooming, as for *Stenocereus griseus* (Piña 1977).

The time between flower bud differentiation and flower opening is relatively short for cacti—30 to 35 days for *Cereus peruvianus* and *Hylocereus* spp. (Nerd and Mizrahi 1997), 40 to 50 days for *Opuntia* spp. (Pimienta-Barrios 1990), 45 to 60 days for *Stenocereus megalanthus* (Nerd and Mizrahi, 1997), and 40 days for *S. queretaroensis* (Pimienta-Barrios and Nobel 1998). This behavior is similar to that for other tropical and subtropical fruit crops, such as orange, avocado, and mango (Pimienta-Barrios 1990), but contrasts with that for temperate fruit crops (e.g., apple, peach, pear) whose flower initiation usually occurs 1 year before flowering (Faust 1989).

Flower bud initiation for *Opuntia* spp. is inhibited by shade and gibberellic acid (GA). Both shade and GA are effective when applied before the vegetative meristem in the areoles begins its transformation to the reproductive condition, as indicated by the flattening of its dome. Areoles in which GA inhibit flower bud differentiation show a marked increase in the number of spines (Pimienta-Barrios 1990), perhaps reflecting a reversion to the juvenile phase, as occurs for *Hedera helix* (Rogler and Hackett 1975).

Low temperatures in the winter influence flower bud burst for some cultivated cacti, indicating that chilling is involved (Nerd and Mizrahi 1997). Horticulturists argue that bud burst occurs at the end of the winter in cultivated cacti. In the highlands of Ayacucho, Peru, flower bud burst occurs throughout the year for *Opuntia ficus-indica,* suggesting that other physiological factors can be involved in the control of flower induction and bud break. Thus, flower bud initiation and control may not rely on a single factor, such as chilling.

The time of flowering in certain species of cacti is little influenced by water availability. For instance, many species of cacti in Mexico and the southwestern United States start flowering (e.g., *Echinocactus platyacanthus,* Trujillo 1982; *Echinocereus* spp., Powell et al. 1991; *Neobuxbaumia* spp., Valiente-Banuet et al. 1997) or have their flowering peaks (e.g., *Ferocactus histrix,* del Castillo 1988a; *Opuntia* spp., Rodríguez-Zapata 1981, del Castillo and González-Espinosa 1988; *Pachycereus pringlei,* Fleming et al. 1994) in March or April. These months are among the driest and near the end of the longest drought period of the year. Although reproductive development occurs during the dry season in arid regions of both the Northern and Southern Hemispheres, relatively few fruits abscise and a high percentage of flowers become fruits. In contrast, the reproductive growth of many other fruit crops is highly sensitive to drought. For instance, the percentage of flowers that become fruit can be 95% for *O. ficus-indica* and 28% for *Stenocereus queretaroenis* but is often under 10% for many fruit crops, such as apple, avocado, mango, and orange (Stephenson 1981; Pimienta-Barrios 1990; Pimienta-Barrios et al. 1995). This may in part reflect the succulence of the cactus stems, which can store appreciable amounts of water that can be available to reproductive structures during drought (Gibson and Nobel 1986).

Reproductive growth for *O. ficus-indica* is highly re-

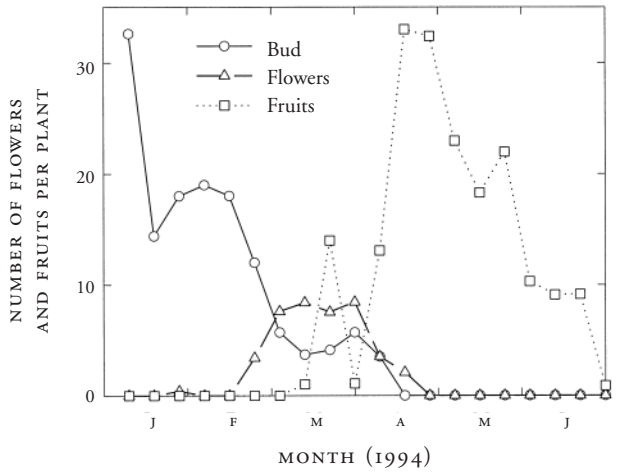


Figure 5.3. Reproductive development for *Stenocereus queretaroensis* under natural conditions, indicating the emerging flower buds (o), open flowers (Δ), and nearly ripe fruits (□). Adapted from Pimienta-Barrios and Nobel (1995).

sponsive to management. Both flower number and fruit number dramatically increase in response to both mineral and organic fertilizers, water, and pruning (Pimienta-Barrios 1990). In contrast, irrigation does not affect stem extension, reproductive demography, fruit quality, or seed size for *S. queretaroensis* (Pimienta-Barrios and Nobel 1995).

The time from flower opening to fruit maturation is relatively short, particularly for columnar cacti. Fertilized flowers give rise to mature fruits 40 to 50 days after pollination for *Pilosocereus lanuginosus, Stenocereus griseus,* and *Subpilocereus repandus* (Petit 1995). For *S. queretaroensis,* fruits attain over 90% of their final length in about 40 days, and the overall development period from anthesis to maturity is about 90 days (Pimienta-Barrios and Nobel 1995). Fruits of the vinelike climbing cacti *Hylocereus costaricencis, H. polyrhizus,* and *H. undatus* have a short growth period of about 50 days, whereas fruits of *Selenicereus megalanthus* require 90 to 150 days (Weiss et al. 1994b, 1995).

Seed Germination

Both ovule fertilization and seed germination are critical stages in plant development. Despite the importance of seed germination in the reproduction of cacti, the pioneer studies on seed germination are relatively recent. Alcorn and Kurtz (1959) and McDonough (1964) revealed the importance of light. But Zimmer (1969) found that some species do not require light for germination and that the cactus species that require light for germination have a greater response when they are exposed to red light. Pilcher (1970) indicated the presence of dormancy for *Opuntia* seeds, an observation later confirmed for a large number of *Opuntia* species (Bregman and Bouman 1983; Pérez 1993). Although most cactus seeds germinate within a week, germination for subfamily Opuntioideae often takes a few months (Bregman and Bouman 1983; Pérez 1993; Table 5.2). Seed dormancy, characterized by the perseverance of the dormant condition even when the seeds are exposed to optimal environmental conditions for germination, has survival value for cacti growing in arid environments. Both innate and enforced dormancy are common for most cacti (Rójas-Aréchiga and Vázquez-Yanes 2000).

A low level of light (PPF < 20 μmol m^{-2} s^{-1}) is required for the germination of most cactus seeds. Red light stimulates germination for soaked seeds of *Stenocereus griseus,* but the effect of red light is reversed by far-red light, suggesting the participation of phytochrome in the seed germination process (Martínez-Holguín 1983). The application of gibberellic acid also increases seed germination for *S. griseus* (Moreno et al. 1992; López-Gómez and Sánchez-Romero 1989). Thus, phytochrome may exert its control of seed germination through the synthesis of gibberellic acid. The seeds of *S. griseus* also maintain their viability after 12 months of storage, reaching germination percentages of 90 to 100% four days after sowing (López-Gómez and Sánchez-Romero, 1989). Maiti et al. (1994) suggest that a high germination percentage is associated with a thin testa and with the presence of starch granules. Seed germination for *Stenocereus queretaroensis* is relatively high even though its seeds are small (2.6 mg); the seeds have a thin testa and a relatively large amount of lipid (Pimienta et al. 1995). Seeds of many wild species that respond to light are also rich in lipids. Because of their small size and light requirements, such seeds should be near the soil surface for successful germination.

Besides light, the germination of cactus seeds requires wet conditions and responds to temperature (Rójas-Aréchiga and Vázquez-Yanes 2000). Water uptake stimulates cracks in the testa (outer seed coat) caused by the growing embryo (Bregman and Bouman 1983) and leaches possible germination inhibitors (Mondragón-Jacobo and Pimienta-Barrios 1995). The presence of soluble inhibitory substances in the testa of cactus seeds maintains the dormant state until environmental conditions are suitable for development (Rójas-Aréchiga and Vázquez-Yanes 2000). The fractional germination of seeds of some cacti increases for the first 3 years after harvest, or after the passage through the digestive tracts of rabbits. Seeds that pass through the digestive tract of cattle exhibit average germination percentages that are 50% higher than seeds re-

TABLE 5.2
Percentage of seed germination of cultivated and wild opuntias species at different times after fruit ripening

	Time (months) after fruit ripening					
Common name (species)	2	4	6	8	12	14
Cultivated						
Burrona (*Opuntia* spp.)	0	0	0	0	3	23
Chapeada (*O. ficus-indica*)	0	0	0	0	28	80
Cristalina (*O.* spp.)	0	0	0	3	85	90
Naranjona (*O. ficus-indica*)	0	0	0	5	42	50
Wild						
Cardona (*O. streptacantha)*	0	0	3	23	40	30
Negrita (*O. streptacantha*)	0	0	13	55	67	100
Tapona (*O. robusta*)	0	0	8	3	80	32

Adapted from Mondragón-Jacobo and Pimienta-Barrios (1995).

moved from ripe fruits (Potter et al. 1984). For cacti, the optimal temperature for seed germination ranges from 17 to 34°C, with a mean of 25°C (Nobel 1988). Alternating temperatures give higher germination yields than constant temperatures (Rójas-Aréchiga and Vázquez-Yanes, 2000). For *Opuntia* species, optimum constant temperatures vary from 25 to 35°C (Mondragón-Jacobo and Pimienta-Barrios 1995). For *Astrophytum myriostigma,* germination rates are highest (80–98%) at temperatures from 20 to 25°C, and decrease at higher temperatures under conditions of diffuse light (Moreno et al. 1995).

For species of *Opuntia* and *Stenocereus,* among others, seed dormancy is apparently related to the time of fruit ripening. For instance, fruit ripening for *S. queretaroensis* and *Myrtillocactus geometrizans* occurs at the end of the spring, in contrast with *Opuntia,* for which fruit ripening for most species occurs from the middle of summer to the beginning of the autumn. The occurrence of fruit ripening at the end of the spring for *S. queretaroensis* and *M. geometrizans* may be optimal, because seed maturation occurs just before the start of the summer, which favors seed germination and establishment because of favorable soil moisture and shading by surrounding natural vegetation in their habitats (Fig. 5.4; Nobel 1988; Pimienta-Barrios and Nobel 1998). In contrast, seed development for *Opuntia* spp. occurs near the middle or the end of the rainy season, so its seed maturation and dispersal coincide with the beginning of the dry season and the reduction of air temperatures in Mexico.

To avoid drought stress and frost damage, seeds of *Opuntia* spp. have dormancy periods of 7 to 8 months; seed germination is initiated at the start of the next rainy season (Pérez 1993). However, seed germination for other cacti indicates that dormancy is not related to the time of fruit ripening. Seeds of some barrel cacti (e.g. *Ferocactus flavovirens, F. histrix, F. latispinus,* and *F. robustus*) and certain columnar cacti (e.g., *Cephalocereus chrysacanthus, Neobuxbaumia,* and *Pachycereus hollianus*) do not show dormancy, as high percentages of their seeds germinate without scarification or washing, once the fruit is mature (Bregman and Bouman 1983; del Castillo 1986b; Rójas-Aréchiga et al. 1998). However, the seeds of *Echinocereus polyacanthus* do not germinate in the winter, at the time of fruit ripening, suggesting that low temperatures or short days can induce dormancy for this species (Trujillo 1982). Given the short and unpredictable rain periods occurring in most arid and semiarid habitats, the absence of dormancy for cactus seeds may be considered a selective advantage, as a quick onset of germination would enable seedling establishment despite an erratic environment.

Apomixis

In addition to sexual reproduction, two types of asexual reproduction are present in cacti: vegetative apomixis and agamospermy. In vegetative apomixis, a new plant is derived after the rooting of plant fragments or ramets detached from a parent plant, as occurs for *Myrtillocactus geometrizans.* Among the Cactaceae, *Opuntia* spp. are probably the best examples of reproductive versatility, using a wide array of sexual and asexual methods. Indeed,

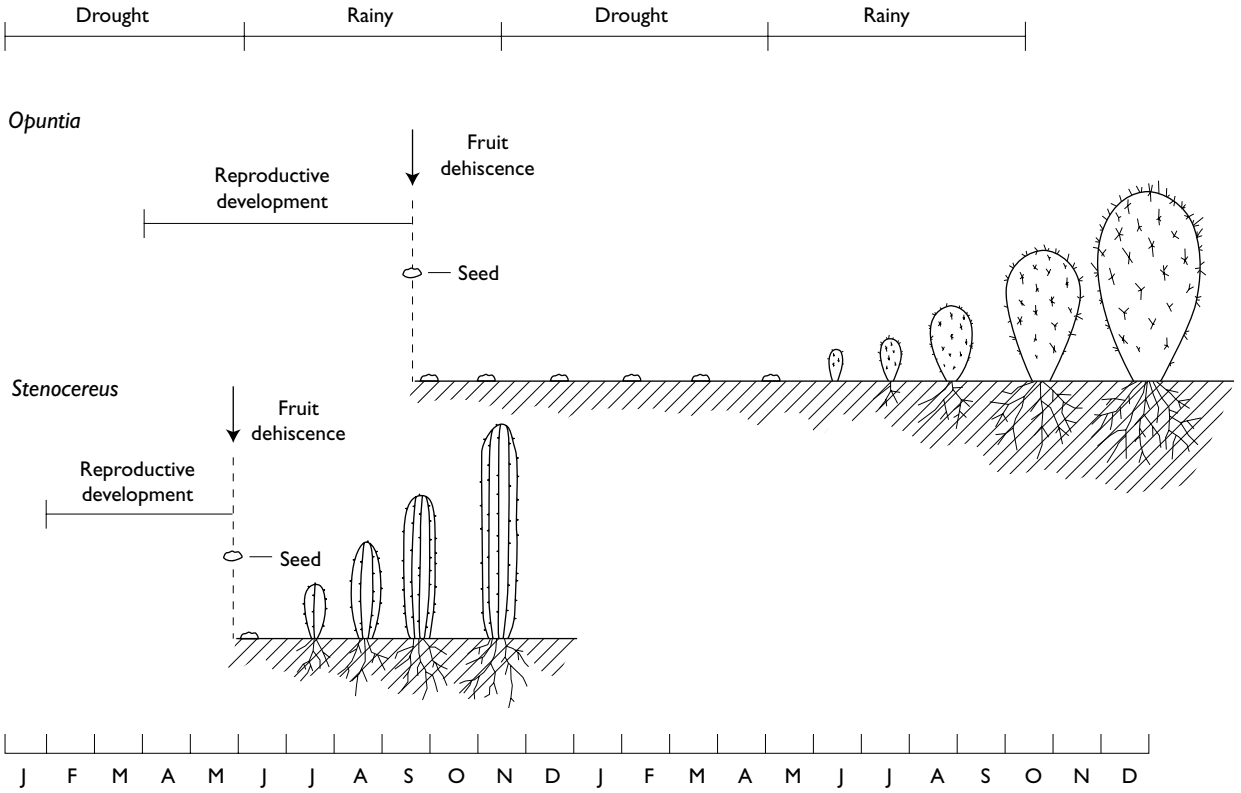


Figure 5.4. The time of reproductive development, fruit dehiscence, and seed germination with respect to drought and rainfall periods for *Opuntia* and *Stenocereus* spp. Adapted from Pimienta-Barrios (1999).

propagation through vegetative parts is common for them in both natural and cultivated populations in arid regions (Grant and Grant 1971; Nava et al. 1981; Pimienta-Barrios 1990; Mandujano et al. 1996, 1998; Negrón-Ortiz 1998). Vegetative apomixis is particularly important, because the propagules carry reserves of water and energy, allowing them to withstand prolonged drought. Indeed, certain species of this genus, especially cylindropuntias, reproduce exclusively or nearly exclusively asexually.

One disadvantage of asexual reproduction can be its low dispersion. In many species of *Opuntia,* however, vegetative apomixis can be highly successful, in part due to its high dispersability. The cladodes of platyopuntias and the joints of cylindropuntias can be readily detached and adhere by means of the spines to the skin of cattle, wild life, and other animals that touch the plants. This favors the invasion of opuntias in overgrazed areas (Anthony 1954). Humans also play an important role in spreading opuntias vegetatively. In semiarid areas of central Mexico, shepherds and cattle ranchers commonly cut off the cladodes of opuntias for animal feeding or to have easy access when walking. Some of the cladodes, or even their fragments, may root and give rise to new individuals. Indeed, nopaleras, a vegetation type in central Mexico dominated by *Opuntia* spp., may be anthropogenic (González-Espinosa 1999). Vegetative apomixis can cause opuntias to become noxious weeds. The epibiotic outbreak of *Opuntia stricta* in Australia after its introduction in 1839 is the best example. In 1920 this species occupied 24×10^6 hectares and was colonizing about 400,000 hectares per year. The moth *Cactoblastis cactorum* was brought from Argentina to control the outbreak (Harper 1977).

Some asexual species of *Opuntia* provide the best examples of high dispersal rates among cacti. *Opuntia fragilis,* for instance, is a low plant, 5 to 10 cm tall, with an enormous geographic range from Chihuahua and Coahuila in Mexico (Bravo-Hollis 1978) up to Saskatchewan, Alberta, and British Columbia in Canada, including 16 states in the United States (Mitch 1970). Its altitudinal range is from sea level up to 2,400 m in a great variety of vegetation types. Flowering and fruit production are rare, and fruits are usually sterile (Benson 1982; Mitch 1970). Bison probably helped to disperse it (Mitch 1970). Another example is *O. polyacantha,* which has sterile fruits, high

phenotypic diversity, and a wide geographic distribution from Chihuahua and Coahuila, Mexico, to Canada (Benson 1982; Mitch 1970).

In certain species of *Opuntia,* sexual reproduction occurs only sporadically. For instance, despite its high seed production, most of the population regeneration of *O. rastrera* is through asexual reproduction (Mandujano et al. 1996), although in grassy areas of its range, *O. rastrera* reproduces mainly sexually (Mandujano et al. 1998). Germination rates for various *Opuntia* spp. are usually low, at least soon after the seed is released (Trujillo and González-Espinosa 1991). Germination rates may increase steadily with aging (Mandujano et al. 1997). However, predation rates in natural habitats may also be high, particularly by rodents (González-Espinosa and Quintana-Ascencio 1986). Thus, mutations favoring asexual reproduction may be common. Indeed, asexual clones can be derived from sexual species. *Opuntia ficus-indica* produces normal seeds, but sterile clones occur in which mutation back to sexual reproduction is possible (Weiss et al. 1993).

Whereas vegetative apomixis is widespread among opuntias and may contribute to their large geographic range, it is less important in the rest of the Cactaceae. For vegetative apomixis to be an efficient means of dispersal, the plants must have small detachable units, as happens for small opuntias, such as *O. fragilis.* In many opuntias with large cladodes, vegetative apomixis may not be an efficient way of reproduction, because sooner or later the limited dispersal would cause the saturation of suitable available habitat (cf. the strawberry-coral model; Williams 1975). In certain species of *Opuntia,* however, humans can circumvent this problem by promoting vegetative reproduction artificially, as may have happened for the Mexican nopaleras. Other cactus genera, such as *Hylocereus,* can be propagated vegetatively (Ortiz-Hernández 1999). However, reproduction by seed is the most common reproductive method for most cacti.

For certain plants, normal seed is set but sexual fusion does not occur. Compared to vegetative apomixis, agamospermy has the advantage of seminifery, because the seed is a vehicle of dispersal that confers resistance to environmental extremes, such as through dormancy (Heslop-Harrison 1983). As for vegetative apomixis, agamospermy is also a common asexual reproduction method for species of *Opuntia* (Ganong 1898; Archibald 1939; Tiagi 1954; Flores and Engleman 1973; García-Aguilar and Pimienta-Barrios 1996; Négron-Ortiz 1998), as well as *Mammillaria* (Ross 1981). Polyembryonic seeds are common in most of the wild and cultivated *Opuntia* spp. growing in semiarid central Mexico (Trujillo and González-Espinosa 1982; Pérez 1993). For example, seeds of many wild opuntias have two and, on rare occasions, three embryos (Trujillo and González-Espinosa 1982), and the percentages of polyembryonic seeds varies from 0.5 to 20% (Pérez 1993). The production of both sexual and asexual seeds may be considered a facultative apomixis, exchanging genetic material by occasionally producing sexual material and achieving a balance between stability and flexibility that permits adaptation to stressful environments.

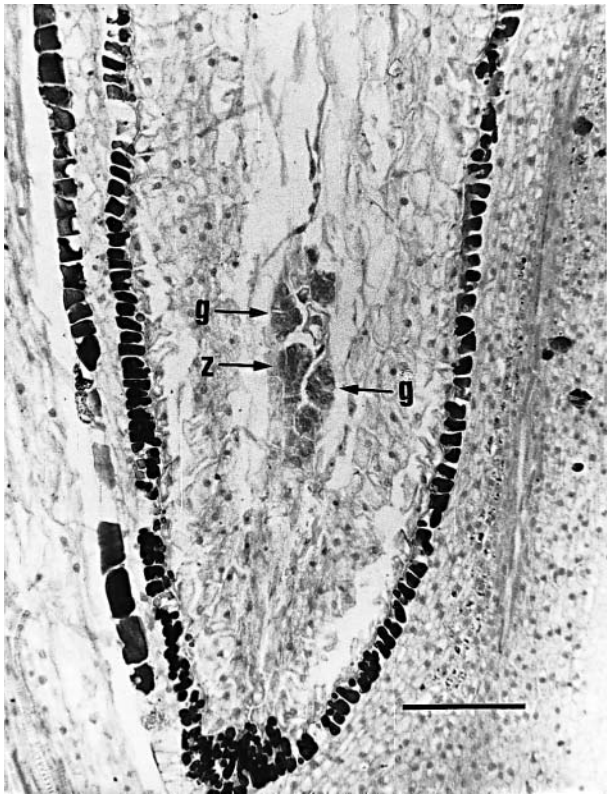


Figure 5.5. Multiple proembryos in the embryos sac of the polyembryonic *Opuntia streptacantha,* showing a laminar zygote proembryo (z) and globular adventitious proembryos (g). Scale bar = 50 µm.

Mammillaria prolifera is apomictic by adventitious embryos. However, some primarily outcrossing (allogamous) taxa, e.g., *Mammillaria tenuis* and *M. zeilmanniana,* are partially apomictic by adventitious embryos after endosperm formation. Self-sterile polyploids of *M. compressa, M. parkinsona,* and *Gymnocalccium brunchii* have extensive vegetative branching. *Opuntia* spp., which have a high frequency of vegetative propagation, adventitious embryos, and self-fertility, have extensive polyploidy (Ross 1981).

Embryos from apomictic seeds generally originate from nuclear tissue, and nuclear embryogenesis commonly occurs without pollination (Tisserat et al. 1979). However, a comparative study of embryo-sac development in a

monoembryonic/polyembryonic *Opuntia* species to assess the cytological origin of both sexual and agamospermic embryos reveals that, in the polyembrionic species, multiple embryos are differentiated in the central cell of the embryo sac at the mycropilar side; however, pollen tubes do not penetrate the mycropile, indicating that fertilization does not occur (García-Aguilar and Pimienta-Barrios 1986). The embryos located at the periphery of the embryo sac are globular and without a suspensor, differing from a well-developed laminar embryo with a well-defined suspensor located at the mycropilar side of the embryo sac (Fig. 5.5). Because of their position in the embryo sac and their morphology, the laminar embryo with its suspensor apparently differentiates from the egg cell, and the globular embryos without suspensors derive from the nuclear cells and further invade the embryo sac (Bhojwani and Bhatnagar 1979; Tisserat et al. 1979). The lack of evidence of meiotic chromosome reduction during megasporogenesis and fertilization in the polyembryonic species suggests that the laminar embryo, with a well-defined suspensor, develops by diplospory-parthenogenesis (gametophytic apomixis), and the globular embryos without suspensors develop by adventitious embryony (Heslop-Harrison 1983).

Conclusions

The reproductive systems of cacti include such striking features as combining of two or more reproductive methods and switching between reproductive modes during the lifetime of an individual. Asexual reproduction can fix favorable combinations of genes, which were produced previously by sexual reproduction. Selfing can be an economic way of sexual reproduction and also functions as a genetic barrier, preventing or reducing hybridization and permitting the production of seed when external pollination is unreliable. Outcrossing is undoubtedly a genetic method favoring the wide diversity observed for cacti. But all of these forms of reproduction have genetic costs (e.g., segregational load with outcrossing, inbreeding depression with selfing, and probably mutational load with asexual reproduction) and ecophysiological costs to the plant (e.g., in a particular outcrossing, attracting pollinators and resource demands). In some cases, the partial or complete suppression of one of these reproductive systems has been successful, as for species with unisexual individuals or the sterile or partially sterile opuntias.

The reproductive versatility is extremely widespread in members of the genus *Opuntia,* and it can play an important role in the ecological strategy of adaptation to aridity. Not surprisingly, *Opuntia* is the most widely distributed genus in the Cactaceae. Members of this genus have self-pollinating as well as cross-pollinating flowers. Both sexual reproduction and asexual reproduction by vegetative parts and seeds occur. These versatile reproductive systems are often controlled by environmental factors, suggesting that the genetic systems may exhibit phenotypic plasticity. Although asexual reproduction can be very successful, in some circumstances sexual reproduction, or the mixed mating system (most likely the ancestral form) with its combination of outcrossing and inbreeding, predominates. The evolutionary importance of sexual reproduction is reflected by its existence, persistence, ubiquity, and presumably lower energy investment, despite the great potential among cacti for asexual reproduction.

Literature Cited

Alcorn, S. M., and E. B. Kurtz. 1959. Some factors affecting the germination of seeds of the saguaro cactus (*Carnegia gigantea*). *American Journal of Botany* 46: 526–529.

Alcorn, S. M., McGegor, S. E., and S. E. Olin. 1961. Pollination of saguaro cactus by doves, nectar feeding bats, and honey bees. *Science* 133: 1594–1595.

Anthony, M. 1954. Ecology of the *Opuntiae* in the Big Bend region of Texas. *Ecology* 35: 334–347.

Archibald, A. E. E. 1939. The development of the ovule and seed of joined cactus (*Opuntia aurantiaca* Lindley). *South African Journal of Science* 36: 195–211.

Arias-Moreno, S. 1997. Distribución general. In *Suculentas Mexicanas Cactáceas.* Editorial CVS Publicaciones, Mexico City. Pp. 17–25.

Arias-Montes, S., and H. Arreola-Nava. 1995. Consideraciones sobre *Opuntia decumbens* Salm-Dick. *Cactáceas y Suculentas Mexicanas* 40: 86–92.

Arreola-Nava, H. 1997. Formas de vida y características morfológicas. In *Suculentas Mexicanas Cactáceas.* Editorial CVS Publicaciones, Mexico City. Pp. 27–35.

Benson, L. 1979. *Plant Classification.* D. C. Heath, Lexington, Massachusetts.

Benson, L. 1982. *The Cacti of the United States and Canada.* Stanford University Press, Stanford, California.

Berry, J. A., I. P. Ting, and E. Zeiger. 1983. The biology of desert plants: Opportunities and needs for basic research. Conference Report, October 24–25, University of California Philip L. Boyd Deep Canyon Desert Research. American Society of Plant Physiologist, Rockville, Maryland.

Bhojwani, S. S., and P. Bhatnagar. 1979. *The Embryology of Angiosperms.* Vikas Publishing House, New Delhi.

Booke, N. H. 1980. Developmental morphology and anatomy in Cactaceae. *BioScience* 30: 605–610.

Bravo-Hollis, H. 1978. *Las Cactáceas de México,* Vol. 1. Universidad Nacional Autónoma de México, Mexico City.

Bregman, R. 1996. The genus Matucana: Biology and systematics of a fascinating Peruvian cactus. A. Balkema, Rotterdam, The Netherlands.

Bregman, R., and F. Bouman. 1983. Seed germination in Cactaceae. *Botanical Journal of the Linnean Society* 86: 357–374.

Britton, N., and J. N. Rose, 1937. *The Cactaceae.* Dover, New York.

Bullock, S. H. 1985. Breeding systems in the flora of a tropical deciduous forest in Mexico. *Biotropica* 17: 287–304.

Buxbaum, F. 1950. *Morphology of Cacti, Section I. Roots and Stems* (Edwin B. Kurtz, ed.). Abbey Garden Press, Pasadena, California.

Cota, J. H., and C. T. Philbrick. 1994. Chromosome number variation and polyploidy in the genus *Echinocerus* (Cactaceae). *American Journal of Botany* 81: 1054–1062.

del Castillo, R. F. 1986a. La selección natural de los sistemas de cruzamiento en *Opuntia robusta.* Master's Thesis, Colegio de Postgraduados, Montecillo, Mexico.

del Castillo, R. F. 1986b. Semillas, germinación y establecimiento de *Ferocactus histrix. Cactáceas y Suculentas Mexicanas* 31: 5–11.

del Castillo, R. F. 1988a. Nota sobre los nectarios extraflorales en cactáceas. *Cactáceas y Suculentas Mexicanas* 33: 99–100.

del Castillo, R. F. 1988b. Fenología y remoción de semillas en *Ferocactus histrix. Cactáceas y Suculentas Mexicanas* 33: 5–14.

del Castillo, R. F. 1994. Polinización y otros aspectos de la biología floral de *Ferocactus histrix. Cactáceas y Suculentas Mexicanas* 39: 36–43.

del Castillo, R. F. 1999. Exploración preliminar sobre los sistemas de cruzamiento en *Opuntia.* In *El Nopal. Memoria, VIII Congreso Nacional y VI Internacional sobre el Conocimiento y Aprovechamiento del Nopal,* Universidad Autónoma de San Luis Potosí, San Luis Potosí, Mexico. Pp. 360–389.

del Castillo, R. F., and M. González-Espinosa. 1988. Una interpretación evolutiva del polimorfismo sexual de *Opuntia robusta* (Cactaceae). *Agrociencia* 71: 185–196.

de Nettancourt, D. 1997. Incompatibility in angiosperms. *Sexual Plant Reproduction* 10: 185–199.

Faust, M. 1989. *Physiology of Temperate Zone Fruit Trees.* Wiley, New York.

Fischer, R. A., and N. C. Turner. 1978. Plant production in the arid and semiarid zones. *Annual Review of Plant Physiology* 29: 277–317.

Fleming, T. H., S. Maurice, S. L. Buchmann, and M. D. Tuttle. 1994. Reproductive biology and relative fitness in a trioecious cactus, *Pachycereus pringlei* (Cactaceae). *American Journal of Botany* 81: 858–867.

Fleming, T. H., S. Maurice, and J. L. Hamrick. 1998. Geographic variation on the breeding system and evolutionary stability in *Pachycereus pringlei* (Cactaceae). *Evolutionary Ecology* 12: 279–289.

Flores, V. M. E., and E. M. Engleman. 1973. Apuntes sobre anatomía y morfología de las semillas de cactáceas. I. Desarrollo y estructura. *Revista de Biología Tropical* 24: 199–207.

Ganong, W. F. 1898. Upon polyembriony and its morphology in *Opuntia vulgaris. Botanical Gazette* 25: 221–228.

García-Aguilar, M., and E. Pimienta-Barrios. 1996. Cytological evidences of agamospermy in *Opuntia* (Cactaceae). *Haseltonia* 4: 39–42.

García-Sánchez, R. 1984. Patrones de polinización y fenología floral en poblaciones de *Opuntia* spp. en San Luis Potosí y Zacatecas, México. Bachelor's Thesis, Universidad Nacional Autónoma de México, Los Reyes Iztacala.

Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer.* Harvard University Press. Cambridge, Massachusetts.

González-Espinosa, M., and P. F. Quintana-Ascencio. 1986. Seed predation and dispersal in a dominant desert plant: *Opuntia,* ants, birds and mammals. In *Frugivores and Seed Dispersal* (A. Estrada and T. H. Fleming, eds.). Dr. D. W. Junk, Dordrecht, The Netherlands. Pp. 273–284.

González-Espinosa, M. 1999. Interacciones entre fenología, elementos bióticos y disturbio por pastoreo en las nopaleras del centro de México. In *El Nopal. Memoria, VIII Congreso Nacional y VI Internacional sobre el Conocimiento y Aprovechamiento del Nopal.* Universidad Autónoma de San Luis Potosí, San Luis Potosí, Mexico. Pp. 342–359.

Grant, B. R., and P. R. Grant. 1981. Exploitation of *Opuntia* cactus by birds on the Galápagos. *Oecologia* 49: 179–187.

Grant, V. K., and W. A. Connell. 1979. The association between Carpophilus beetles and cactus flowers. *Plant Systematics and Evolution* 133: 99–102.

Grant, V. K., and K. A. Grant. 1971. Dynamics of clonal microspecies in Cholla cactus. *Evolution* 25: 144–155.

Grant, V. K., and K. A Grant. 1979a. Pollination of *Echinocereus fasciculatus* and *Ferocactus wislizenii. Plant Systematics and Evolution* 132: 85–90.

Grant, V. K., and K. A. Grant. 1979b. Pollination of *Opuntia basiliaris* and *O. littoralis. Plant Systematics and Evolution* 132: 321–325.

Grant, V. K., and K. A. Grant. 1979c. The pollination spectrum in the Southwestern American cactus flora. *Plant Systematics and Evolution* 133: 29–37.

Grant, V. K., and P. D. Hurd. 1979. Pollination of the Southwestern Opuntias. *Plant Systematics and Evolution* 133: 15–28.

Grant, V. K., K. A. Grant, and P. D. Hurd. 1979. Pollination of *Opuntia lindheimeri* and related species. *Plant Systematics and Evolution* 132: 313–320.

Grayum, M. H. 1991. Systematic embryology of the Araceae. *Botanical Review* 57: 167–203.

Harper, J. L. 1977. *Population Biology of Plants.* Academic Press, New York.

Heslop-Harrison, J. 1983. The reproductive versatility of flowering plants: An overview. In *Strategies of Plant Reproduction* (W. J. Meudt, ed.). Beltsville Symposia in Agricultural Reseach. Allanheld, Osmun/Granada, London. Pp. 3–18.

Leuck E. E., and J. M. Miller. 1982. Pollination biology and chemotaxonomy of the *Echinocereus viridiflorus* complex (Cactaceae). *American Journal of Botany* 69: 1669–1672.

Lewis, D. 1979. *Sexual Incompatibility in Plants.* Edward Arnold, London.

Lewis, W. H. 1980. Polyploidy in Angiosperms. Dicotyledons. In *Polyploidy, Biological Relevance* (D. H. Lewis, ed.). Plenum Press, New York. Pp. 110–120.

Linskens, F. H. 1983. Pollination processes: Understanding fertilization and limits to hybridization. In *Strategies of Plant Reproduction* (G. W. J. Meudt, ed.). Beltsville Symposium in Agricultural Research. Allanheld, Osmund/Granada, London. Pp. 35–49.

Lomelí, M. E., and E. Pimienta. 1993. Demografía reproductiva del pitayo (*Stenocereus queretaroensis* (Web.) Buxbaum). *Cactáceas y Suculentas Mexicanas* 38: 13–20.

López-Gómez, R., and P. Sánchez-Romero. 1989. Germinación de dos variedades de pitayo *Stenocereus griseus* (Haworth) Buxbaum. *Cactáceas y Suculentas Mexicanas* 34: 35–41.

Maiti, R. K., J. L. Hernández-Piñero, and M. Valdez-Marroquín. 1994. Seed ultrastructure and germination of some species of Cactaceae. *Phyton* 55: 97–105.

Mandujano, M. C., C. Montaña, I. Mendez, and L. Eguiarte. 1996. Reproductive ecology and inbreeding depression in *Opuntia rastrera* (Cactaceae) in the Chihuahuan Desert. Why are sexually derived recruitments so rare? *American Journal of Botany* 83: 63–70.

Mandujano, M. C., J. Golubov, and C. Montaña. 1997. Dormancy and endozoochorus dispersal of *Opuntia rastrera* seeds in the southern Chihuhuan Desert. *Journal of Arid Environments* 36: 259–66.

Mandujano, M. C., C. Montaña, I. Mendez, and J. Golubov. 1998. The relative contribution of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. *Journal of Ecology* 86: 911–921.

McDonough, W. 1964. Germination responses of *Carnegia gigantea* and *Lemairocereus thurberi. Ecology* 45: 155–159.

McMillan, A. J. S., and J. B Horobin. 1995. *Christmas Cacti: The Genus* Schlumbergera *and Its Hybrids.* Royal Botanical Gardens, Kew, England.

Mitch, L. W. 1970. Wyoming native cacti. *Cactus and Succulent Journal (U.S.)* 42: 155–159.

Mondragón-Jacobo, C., and E. Pimienta-Barrios. 1995. Propagation. In *Agro-Ecology, Cultivation, and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 64–70.

Moreno, N. P., López, J. J., and L. Arce. 1992. Aspectos sobre las semillas y su germinacion de *Echinomastus mariposensis* Hester. *Cactáceas y Suculentas Mexicanas* 37: 21–27.

Nassar, M. J., N. Ramírez, and O. Linares. 1997. Comparative pollination biology of Venenzuelan columnar cacti and the role of nectar-feeding bats in their sexual reproduction. *American Journal of Botany* 84: 918–927.

Nava, R. C., J. J. López G., and J. Gasto, C. 1981.

Dinámica poblacional del ecosistema natural de *Opuntia streptacantha* Lemaire. *Monografía Técnica Científica, Serie Recursos Naturales, Universidad Autónoma Agraria Antonio Narro* 7: 219–271.

Negrón-Ortiz, V. 1998. Reproductive biology of a rare cactus, *Opuntia spinosissima* (Cactaceae), in the Florida Keys: Why is seed set very low? *Sexual Plant Reproduction* 11: 208–221.

Nerd, A., and Y. Mizrahi. 1997. Reproductive biology of cactus fruit crops. *Horticultural Reviews* 16: 321–346.

Nobel, P. S. 1995. Environmental biology. In *Agro-Ecology, Cultivation, and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 36–48.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Ortega, C. M. M. 1993. Diferenciación de los gametofitos masculino y femenino en pitayo (*Stenocereus queretaoensis* (Weber) Buxbaum) y su relación con aspectos evolutivos. Bachelor's Thesis, Universidad de Guadalajara, Guadalajara, Mexico.

Ortíz-Hernández, Y. D. 1999. *Pitahaya. Un nuevo Cultivo para México.* Editorial Limusa, Mexico City.

Osborn, M. M., P. G. Kevan, and M. A. Lanen. 1988. Pollination biology of *Opuntia polyacantha* (Cactaceae) in southern Colorado. *Plant Systematics and Evolution* 159: 85–94.

Pérez, R. C. 1993. Viabilidad de semillas y poliembrionía en morfoespecies silvestres y cultivadas de *Opuntia* spp. Bachelor's Thesis, Universidad de Guadalajara, Guadalajara, Mexico.

Petit, S. 1995. The pollinators of two species of columnar cacti on Curaçao, Netherlands Antilles. *Biotropica* 27: 538–541.

Pickett, C. H., and W. D. Clark. 1979. The function of extrafloral nectaries in *Opuntia acanthocarpa* (Cactaceae). *American Journal of Botany* 66: 618–625.

Pilcher, B. L. 1970. Germination of seeds of four species of *Opuntia. Cactus and Succulent Journal (U.S.)* 42: 281–282.

Pimienta-Barrios, E. 1990. *El Nopal Tunero.* Universidad de Guadalajara, Zapopan, Mexico.

Pimienta-Barrios, E. 1999. *El Pitayo en Jalisco y Especies Afines en Mexico.* Universidad de Guadalajara, Zapopan, Mexico.

Pimienta-Barrios, E., and P. S. Nobel. 1995. Reproductive characteristics of pitayo (*Stenocereus queretaroensis*) and their relationships with soluble sugars and irrigation. *Journal of the American Society for Horticultural Science* 120: 1082–1086.

Pimienta-Barrios, E., and P. S. Nobel. 1998. Vegetative, reproductive, and physiological adaptations to aridity of pitayo (*Stenocereus queretaroensis,* Cactaceae). *Economic Botany* 52: 401–411.

Pimienta-Barrios, E., C. Robles-Murguía, and A. Domínguez de la Torre. 1995. Estrategias fisiológicas y reproductivas de adaptación del pitayo a la aridez. *Ciencia* 46: 339–349.

Piña, L. I. 1977. Pitayas y otras cactáceas afines del Estado de Oaxaca. *Cactáceas y Suculentas Mexicanas* 22: 3–14.

Pinkava, D. J., L. A. McGill, and T. Reeves. 1977. Chromosome numbers in some cacti of western North America—III, with nomenclature changes. *Bulletin of the Torrey Botanical Club* 104: 105–110.

Pinkava, J. D., M. A. Baker, B. D. Parfitt, and M. W. Mohlenbrock. 1985. Chromosome numbers in some cacti of western North American—V, with nomenclature changes. *Systematic Botany* 10: 471–483.

Porsch, O. 1938. Das Bestäubunsleben der Kakteenblüte, I. Cactaceae. *Jahrbuch Deutsche Kakteen-Gesellschaft* 1938: 1–80.

Porsch, O. 1939. Das Bestäubunsleben der Kakteenblüte, II. Cactaceae. *Jahrbuch Deutsche Kakteen-Gesellschaft* 1939: 81–142.

Potter, I. R., J. L. Petterson, and D. N. Ueckert. 1984. Germination response of *Opuntia* spp. to temperature, scarification, and other seed treatments. *Weed Science* 32: 106–110.

Powell, J. R., A. D. Zimmerman, and R. A. Hilsenbeck. 1991. Experimental documentation of natural hybridization in Cactaceae: Origin of Lloyd's Hedgehog cactus, *Echinocereus lloydii. Plant Systematics and Evolution* 178: 107–122.

Primack, R. B. 1982. Longevity of individual flowers. *Abstracts, Annual Meeting of the Botanical Society of America.* University of California, Davis. P. 41.

Ramírez, N., and P. E. Berry. 1995. Producción y costo de frutos y semillas entre modos de polinización en 232 especies de plantas tropicales. *Revista de Biología Tropical* 43: 51–159.

Ramírez-Mireles, F. J. 1999. Caracterización y compatibilidad en pitahaya. Bachelor's Thesis, Universidad Autónoma Chapingo, Chapingo, Mexico.

Rodríguez-Zapata, O. 1981. Fenología reproductiva y aporte de frutos y semillas en dos nopaleras del Altiplano Potosino-Zacatecano. Bachelor's Thesis, Universidad Autónoma de Nuevo León, Monterrey, Mexico.

Rogler, L. E., and W. P. Hackett. 1975. Nutrient diversion: An hypothesis to explain the chemical control of flowering. *HortScience* 12: 220–222.

Rójas-Aréchiga, M., C. Vázquez-Yanes, and A. Orozco-Segovia. 1998. Seed response to temperature of two life forms of Mexican cacti species: An ecophysiological interpretation. *Plant Ecology* 135: 207–214.

Rójas-Aréchiga, M., and C. Vázquez-Yanes. 2000. Cactus seed germination: A review. *Journal of Arid Environments* 44: 85–104.

Rosas, C. M. P. 1984. Polinización y fase progámica en *Opuntia* spp. Bachelor's Thesis, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Mexico.

Rosas, C. M. P., and E. Pimienta. 1986. Polinización y fase progámica en nopal (*Opuntia ficus-indica* (L.) Miller). *Tunero Fitotecnia* 8: 164–176.

Ross, R. 1981. Chromosome counts, cytology, and reproduction in the Cactaceae. *American Journal of Botany* 68: 463–70.

Rowley, G. 1980. Pollination syndromes and cactus taxonomy. *Cactus and Succulent Journal (Great Britain)* 42: 95–98.

Roy, B. A., and R. E. Widmer. 1999. Floral mimicry: A fascinating yet poorly understood phenomenon. *Trends in Plant Science* 4: 325–330.

Sosa, R., and C. A. Acosta. 1966. Poliploidia en *Opuntia. Agrociencia* 1: 100–106.

Stephenson, A. G. 1981. Flower and fruit abortion: Proximate and ultimate functions. *Annual Review of Ecology and Systematics* 12: 253–279.

Tiagi, D. Y. 1954. Studies in the floral morphology of *Opuntia dilleni* Haworth. *Botaniska Notiser* 4: 343–356.

Tisserat, B., E. B. Esan, and T. Murashige. 1979. Somatic embryogenesis in angiosperms. *Horticultural Reviews* 1: 1–78.

Toumey, J. W. 1895. Vegetal dissemination of the genus *Opuntia. Botanical Gazette* 20: 356–361.

Trujillo, A. S. 1982. Estudio sobre algunos aspectos ecológicos de *Echinocactus platyacanthus* Lk & O. en el estado de San Luis Potosí. Bachelor's Thesis, Universidad Nacional Autónoma de México, Iztacala.

Trujillo, A. S., and M. González-Espinosa. 1991. Hibridación, aislamiento reproductivo y formas de reproducción en *Opuntia* spp. *Agrociencia, Serie Recursos Naturales Renovables* 1: 39–58.

Valiente-Banuet, A., A. Rójas-Martínez, A. M. del Coro, and P. Davila. 1997. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacán Valley, Central Mexico. *American Journal of Botany* 84: 452–455.

Weiss, J., A. Nerd, and Y. Mizrahi. 1993. Vegetative parthenocarpy in the cactus pear *Opuntia ficus-indica* (L.) Mill. *Annals of Botany* 72: 521–526.

Weiss, J., A. Nerd, and Y. Mizrahi. 1994a. Flowering and pollination requirements in climbing cacti with fruit crop potential. *HortScience* 29: 1487–1492.

Weiss, J., A. Nerd, and Y, Mizrahi. 1994b. Flowering and pollination requirements in *Cereus peruvianus* cultivated in Israel. *Journal of Plant Science* 42: 149–158.

Weiss, J., L. Scheinvar, and Y. Mizrahi. 1995. *Selenicereus megalanthus* (the yellow pitaya), a climbing cactus from Colombia and Peru. *Cactus and Succulent Journal (U.S.)* 67: 280–283.

Williams, G. C. 1975. *Sex and Evolution.* Princeton University Press, Princeton, New Jersey.

Zappi, D.C. 1994. Pilosocereus *(Cactaceae): The Genus in Brazil.* Royal Botanical Gardens, Kew, England.

Zimmer, K. 1969. Über die Keimung von Kakteensamen III. Die Bedeutung des Lichtes. *Kakteen und andere Sukkulenten* 20: 114–147.

CHAPTER

› 6 ‹

POPULATION AND COMMUNITY ECOLOGY

Alfonso Valiente-Banuet and Héctor Godínez-Alvarez

Introduction
Population Ecology
Seed Germination
Seedling Establishment and Growth
Reproduction and Breeding Systems
Seed Dispersal
Population Dynamics
Community Ecology
Conclusions and Future Prospects
Literature Cited

Introduction

Cacti are a typical component of vegetation in tropical and subtropical America (Gibson and Nobel 1986; Barthlott and Hunt 1993; Valiente-Banuet et al. 1995a). Although some species reach high latitudes in British Columbia and Alberta in Canada and in the Patagonian region of Argentina, species diversity increases considerably toward the tropics, Mexico being the most important center with about 850 species and 54 genera (Bravo-Hollis 1978; Arias 1993). The tribes Opuntieae, Cacteae, and Echinocereeae, including species with laterally flattened stems in the genus *Opuntia,* globose or barrel cacti in the genera *Coryphantha, Echinocereus, Mammillaria,* and many monospecific genera such as *Ariocarpus, Astrophytum, Aztekium,* and *Lophophora,* are widely distributed in the Chihuahuan Desert of Mexico with almost 400 endemic species (Arias 1993). In the Sonoran Desert, seven species of columnar cacti (tribe Pachycereeae) with genera such as *Carnegiea, Pachycereus,* and *Stenocereus* dominate the arid landscapes in northwestern Mexico, forming the sarcocaulescent desert of Shreve (1951), which also has many species of cylindropuntias and barrel cacti (Turner et al. 1995). In south-central Mexico in the Balsas River Basin and the Tehuacán Valley, the tribe Pachycereeae with its arborescent cacti is highly diversified; this tribe contains 45 of the 70 species of local columnar cacti in Mexico, constituting the principal structural and floristic elements of columnar-cactus forests (Valiente-Banuet et al. 1995a, 1996). Other tribes, such as Hylocereeae, are basically restricted to humid tropical regions in southeastern Mexico and Central America and are represented mostly by epyphitic cacti (Arias 1993). The genus *Pereskia* is an important component of the tropical deciduous forest of southern Oaxaca, Mexico (Bravo-Hollis 1978).

In these geographical areas, cacti show a considerable diversity of life form, and the different types of vegetation acquire their names depending on their physiognomic

and/or structural dominance (Miranda and Hernández 1963; Rzedowski 1978; Osorio et al. 1996). Spectacular examples of these plant associations include the Cardonales, dominated by columnar cacti called "cardones" since the Spanish conquest times, belonging to the genera *Stenocereus, Pachycereus, Cephalocereus,* and *Mitrocereus;* the Nopaleras, a name derived from the term "nopal," which is the Nahuatl name for the flat-stemmed species of *Opuntia,* consist of dense stands of several species, and "Tetecheras" and "Giganteras," which are dominated by different species of *Neobuxbaumia.* The key aspects in the population and community ecology of these plants are considered in this chapter to determine how abiotic and biotic factors interact to influence the distribution and abundance of a particular species, leading to particular survivorship, fecundity, growth patterns, and groups of species, with an emphasis on the maintenance of biodiversity.

Population Ecology

Cacti have lifespans of decades to hundreds of years (Steenbergh and Lowe 1977). Along their life cycle, the different stages, such as the seed and seedling, juvenile, mature, and senile plants, are exposed to different mortality factors related to high radiation levels, water stress, and biotic interactions such as predation and competition. Early stages of the life cycle are the most important for maintaining viable populations in the field (Steenbergh and Lowe 1969, 1977; Valiente-Banuet and Ezcurra 1991; Godínez-Alvarez et al. 1999). Therefore, the successful production of seeds, their dispersal and germination, seedling establishment, and the survivorship of seedlings and juveniles are essential for the maintenance of cactus populations under natural conditions. These stages constitute a link between the reproductive adults and the new individuals (Howe and Smallwood 1982); thus, the main goal of this section is to analyze their relative effect on the population dynamics of cacti.

Seed Germination

Most studies analyzing seed germination of cactus species have been conducted under controlled conditions in the laboratory (Chapter 5) and few have considered seed germination under field conditions. Dubrovsky (1996, 1998) reported that the seeds of the Sonoran Desert cacti *Carnegiea gigantea, Ferocactus peninsulae, Pachycereus pecten-aboriginum, Stenocereus gummosus,* and *S. thurberi,* subjected to hydration-dehydration cycles of different lengths, germinated faster and accumulated higher biomass compared to untreated seeds. Thus, seeds apparently retain during dehydration the physiological changes promoted by seed hydration. This "seed hydration memory" may facilitate seed germination, increasing the survival of cacti in the field (Dubrovsky 1996).

Light stimulates seed germination for only some species (Table 6.1). Rojas-Aréchiga et al. (1997) divided cacti into two groups: (1) globose or barrel cacti such as *Mammillaria, Echinocactus,* and *Ferocactus* that require light for the seed germination (i.e., positively photoblastic), and (2) columnar cacti in the genera *Neobuxbaumia, Cephalocereus, Pachycereus,* and others for which seed germination is not affected by light. This correlation between light and lifeform in cacti may result from the environmental and maternal effects on seeds during their development (Rojas-Aréchiga et al. 1997). Light requirements are also affected by temperature regimes, washing of the seeds, and gibberellic acid (Rojas-Aréchiga and Vázquez-Yanes 2000). Ecologically, lack of light can inhibit germination when the seeds are deep in the soil, and light can stimulate germination when soil moisture is available (Kigel 1995). Germination occurs for a wide range of temperatures, 10 to 40°C (Nobel 1988; Rojas-Aréchiga and Vázquez-Yanes 2000). The optimal temperature for germination is 20 to 30°C. In addition to these responses, extreme temperatures and aging of seeds decrease germination (Nobel 1988; Rojas-Aréchiga and Vázquez-Yanes 2000).

Seedling Establishment and Growth

The establishment phase and early seedling growth in deserts occurs under unpredictable conditions of precipitation and in soils with high temperatures and low water content. Under these circumstances, cacti are often established beneath the canopy of perennial "nurse plants" (Table 6.2), which modify the environment beneath their canopies. Nurse plant phenomenon have been addressed by determining the spatial relationships between cacti and perennial plants through nearest-neighbor analysis. Both positive and negative effects for cacti are derived from the association with nurse plants, as evidenced by means of a cost-benefit analysis (Franco and Nobel 1989). Among the positive effects of nurse plants on seeds and seedlings is protection against direct solar radiation, leading to a decrease in extreme soil temperatures and hence increasing the soil moisture available for seed germination and early seedling survival (Turner et al. 1966; Steenbergh and Lowe 1969, 1977; Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991; Nolasco et al. 1997). Surface temperatures in open spaces between nurse plants can be up to 65°C, whereas in the shaded microsites under nurse plants soil surface temperatures are 10 to 20°C lower (Turner et al.

TABLE 6.1
Effect of light and temperature on seed germination of some cactus species

Species	Light[1]	Temperature[2]		
		Minimum	*Optimum*	*Maximum*
Cephalocereus chrysacanthus	0	10	30	40
Coryphantha pallida			17–25	
Echinocactus platyacanthus	+	15	25	40
Ferocactus flavovirens	+	15	15–25	40
F. recurvus	+	15	25	40
F. robustus	+	15	30	35
Myrtillocactus geometrizans			17–25	
Neobuxbaumia tetetzo	0	10	15–30	40
Opuntia puberula		17	20–25	
Pachycereus hollianus	0	10	15–20	40
P. pringlei	0			
Stenocereus thurberi	0			

1. Indifferent to light (0) or positively photoblastic (+). References: Nolasco et al. (1996, 1997) and Rojas-Aréchiga et al. (1997).
2. Temperatures (°C) at which minimum, optimum, and maximum germination are observed. References: Godínez-Alvarez and Valiente-Banuet (1998), Nolasco et al. (1996), and Rojas-Aréchiga et al. (1998).

1966; Franco and Nobel 1989; Valiente-Banuet et al. 1991a; Arriaga et al. 1993; Suzán et al. 1996). Nurse plants can also provide protection against wintertime low temperatures, decreasing the susceptibility of seedlings to frost injury (Brum 1973; Steenbergh and Lowe 1969, 1977) and enhancing the establishment of *C. gigantea* and *S. thurberi* in marginal populations where seedlings are exposed to extreme low temperatures during the winter (Brum 1973; Steenbergh and Lowe 1969, 1977; Parker 1987).

Some nurse plants in arid ecosystems increase the nitrogen content of soils under their canopies compared to open spaces. This increment in soil nitrogen, which can reflect interactions with soil microorganisms, creates "islands of fertility" in which the growth rates of seedlings and their survival probability increase (García-Moya and McKell 1970; Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991; Godínez-Alvarez and Valiente-Banuet 1998). Nevertheless, the empirical evidence on the increase of soil nitrogen content is controversial, as some studies support this hypothesis (García-Moya and McKell 1970; Franco and Nobel 1989) whereas others do not (Valiente-Banuet et al. 1991a,b; Arriaga et al. 1993).

Protection against seed and seedling predators is another benefit associated with nurse plants (Steenbergh and Lowe 1969, 1977; McAuliffe 1984a; Hutto et al. 1986; Valiente-Banuet and Ezcurra 1991). Birds, mammals, and insects are among the main cactus predators; however, the protection provided by nurse plants against predators and therefore on the survival of seeds and seedlings depends on the foraging patterns of each predator (Hutto et al. 1986). In this respect, Valiente-Banuet and Ezcurra (1991) found that the seeds of *Neobuxbaumia tetetzo* are similarly predated by harvester ants and ground-foraging birds under nurse plants and in open spaces. On the other hand, McAuliffe (1984a) found that herbivores consume less *Mammillaria microcarpa* and *Echinocereus engelmannii* growing under the canopies of the tree-like cactus *Opuntia fulgida,* because spiny nurse plants inhibit the foraging beneath their canopies.

Among negative effects, nurse plants reduce the photosynthetic photon flux (PPF) and increase the competition for limited supplies of water (Franco and Nobel 1989). For instance, the nurse plants of young *C. gigantea* and *Ferocactus acanthodes* reduce the total daily available PPF by about 70%. This reduction reduces net CO_2 uptake, decreasing the growth rate compared to seedlings in open spaces. Moreover, the competition between seedlings and nurse plants for water can also affect seedling growth. However, such negative effects can be offset by increases in soil fertility under the canopies of nurse plants (Franco and Nobel 1989). Additionally, Altesor et al. (1992) indicate that during the first 10 to 20 weeks after germination, seedlings

TABLE 6.2
Species of cacti and their nurse plants

Species	Nurse plant(s)	Reference
Carnegiea gigantea	*Ambrosia deltoidea* *Cercidium microphyllum* *Encelia farinosa* *Larrea tridentata* *Olneya tesota* *Prosopis juliflora*	Steenbergh and Lowe (1969); Hutto et al. (1986); Franco and Nobel (1989)
Cephalocereus hoppenstedtii	*Caesalpinia melanadenia*	Valiente-Banuet et al. (1991a)
Coryphantha pallida	*Castela tortuosa* *Eupatorium odoratum*	"
Echinocereus engelmannii	*Opuntia fulgida*	McAuliffe (1984a)
Echinomastus erectocentrus	*Celtis pallida* *Lycium andersonii* *L. berlandieri* *Olneya tesota* *Zizyphus obtusifolia*	Suzán et al. (1996)
Ferocactus acanthodes	*Ambrosia dumosa* *Ephedra aspera* *Pleuraphis rigida*	Franco and Nobel (1989)
F. peninsulae	*Haematoxylon brasiletto*	Arriaga et al. (1993)
Lophocereus schottii	*Celtis pallida* *Lycium andersonii* *L. berlandieri* *Olneya tesota* *Zizyphus obtusifolia*	Suzán et al. (1996)
Mammillaria casoi	*Caesalpinia melanadenia*	Valiente-Banuet et al. (1991a)
M. collina	*Castela tortuosa* *Eupatorium odoratum*	"

of *Ferocactus recurvus, Neobuxbaumia tetetzo,* and *Opuntia pilifera* exhibit a C_3 metabolism, which can increase the seedling growth rate during this phase and partially compensate for the lower PPF levels.

Because suitable conditions for seed germination and seedling establishment for many cactus species occur beneath the canopies of nurse plants, cacti can have a clumped distribution pattern in association with trees and shrubs. Moreover, plants may interact competitively with individuals of their own species (i.e., intraspecific competition) and/or with their nurse plants (i.e., interspecific competition). *Carnegiea gigantea* competes intraspecifically, affecting the rate of water uptake, the relative amount of stored water, apical growth, and the reproductive potential (McAuliffe and Janzen 1986). Interspecific competition between cacti and their nurse plants has been reported for *C. gigantea* and *Cercidium microphyllum* in the Sonoran Desert (McAuliffe 1984b) and for *Neobuxbaumia tetetzo* and *Mimosa luisana* in the Tehuacán Valley (Valiente-Banuet et al. 1991b; Flores-Martínez et al. 1998). The intensity of this interaction between cacti and their nurse plants varies with the age of both interactants as well as among dry and wet years, leading to the eventual elimination of either species depending on which had a competitive advantage (McAuliffe 1984b; Valiente-Banuet et al. 1991b; Flores-Martínez et al. 1998).

TABLE 6.2. *(continued)*

Species	Nurse plant(s)	Reference
M. microcarpa	*Opuntia fulgida*	McAuliffe (1984a)
M. thornberi	*Celtis pallida* *Lycium andersonii* *L. berlandieri* *Olneya tesota* *Zizyphus obtusifolia*	Suzán et al. (1996)
Neobuxbaumia tetetzo	*Caesalpinia melanadenia* *Castela tortuosa* *Eupatorium odoratum*	Valiente-Banuet et al. (1991a)
Opuntia leptocaulis	*Larrea tridentata*	Yeaton (1978)
Peniocereus greggii	*Celtis pallida*	Suzán et al. (1996)
P. striatus	*Lycium andersonii* *L. berlandieri* *Olneya tesota* *Zizyphus obtusifolia*	"
Stenocereus thurberi	*Haematoxylum brasiletto* *Jatropha vernicosa* *Tecoma stans*	Arriaga et al. (1993)
Trichocereus pasacana	*Aphyllocladus spartioides* *Larrea divaricata* *Prosopis ferox*	De Viana (1997)
Tumamoca macdougallii	*Celtis pallida* *Lycium andersonii* *L. berlandieri* *Olneya tesota* *Zizyphus obtusifolia*	Suzán et al. (1996)

Reproduction and Breeding Systems

Among flowering plants, the Cactaceae have flowers that are strongly associated with animals, such as bees, hawkmoths, hummingbirds, and bats (Porsch 1939; Grant and Grant 1979; Gibson and Nobel 1986; Valiente-Banuet et al. 1996; Chapter 5). Plant-pollinator relationships are specialized for some cactus species, such as for opuntias with large solitary, diurnal, bowl-shaped flowers adaptable to bee pollination. Bee fauna in the Chihuahuan Desert of Mexico, where opuntia species are highly diversified, is particularly rich with at least 90 species of bees visiting opuntia flowers in North America (Grant and Hurd 1979). Other species pollinated by bees belong to tribe Pachycereeae, such as *Myrtillocactus geometrizans.*

Tubular, red, hummingbird-pollinated flowers are common in Andean and tropical American cacti, especially in genera such as *Rathbunia, Peniocereus, Nopalea,* and *Pachycereus* (Gibson and Nobel 1986). The hawkmoth-flower syndrome—characterized by strongly scented night-blooming flowers with white or whitish perianths and long, slender nectar-containing floral tubes—occurs in species of *Acanthocereus, Cereus, Epiphyllum, Selenicereus,* and *Trichocereus* (Grant and Grant 1979). The bat-flower syndrome—consisting of nocturnal anthesis, whitish bowl-shaped flowers with a strong unpleasant odor at night, large quantities of pollen and nectar, many anthers, and large-mouthed and strong single flowers (Faegri and van der Pijl 1979; Grant and Grant 1979)—occurs for about 70% of columnar cacti in tribe Pachycereeae (Valiente-Banuet et al. 1995a, 1996). Most such species studied in

TABLE 6.3
Pollinators of native columnar cacti (tribes Pachycereeae and Cereeae)

Locality	Species	Pollinator(s)	Reference
Extratropical, northwestern Mexico	*Carnegiea gigantea*	Bees, bats, and birds	Alcorn et al. (1961)
	Lophocereus schottii	Moths	Fleming and Holland (1998)
	Pachycereus pringlei	Bats, birds, and bees	Fleming et al. (1996)
	Stenocereus thurberi	Birds, bats, and bees	Alcorn et al. (1962)
Tropical, southcentral Mexico	*Cephalocereus columna-trajani*	Bats	A. Valiente-Banuet, Ma. Del Arizmendi, A. Casas, and A. Rojas-Martínez (unpublished observations)
	Mitrocereus fulviceps	Bats	"
	Myrtillocactus geometrizans	Bees	"
	Neobuxbaumia macrocephala	Bats	Valiente-Banuet et al. (1997a)
	N. mezcalaensis	Bats	"
	N. tetetzo	Bats	Valiente-Banuet et al. (1996)
	Pachycereus hollianus	Bats	S. Dar, A. Valiente-Banuet, and Ma. Del Arizmendi (unpublished observations)
	P. marginatus	Hummingbirds	"
	P. weberi	Bats	Valiente-Banuet et al. (1997b)
	Pilosocereus chrysacanthus	Bats	"
	Stenocereus pruinosus	Bats	V. Cortés, A. Valiente-Banuet, and A. Rojas-Martínez (unpublished observations)
	S. stellatus	Bats	Casas et al. (1999)
Tropical, northwestern Venezuela	*Pilosocereus lanuginosus*	Bats	Petit (1995)
	P. moritzianus	Bats	Nassar et al. (1997)
	Stenocereus griseus	Bats	"
	Subpilocereus horrispinus	Bats	"
	S. repandus	Bats	"
Tropical, southern Peru	*Weberbauerocereus werberbaueri*	Hummingbirds and bats	Sahley (1996)

All breeding systems are monoecious, except trioecious for *P. pringlei* and andredioecious for *N. mezcalaensis*.

North America are self-incompatible and produce fruits only in presence of nectar-feeding bats (Table 6.3), such as *Choeronycteris mexicana, Leptonycteris curasoae,* and *L. nivalis* (Valiente-Banuet et al. 1996, 1997a,b).

An apparent dichotomy occurs within and outside the tropics among columnar cacti with "bat-pollinated" flowers (Valiente-Banuet et al. 1997a,b), in which *C. gigantea, P. pringlei,* and *S. thurberi* at latitudes above 29° N are pollinated by a wide spectrum of animals, including birds, bats, and bees (Fleming et al. 1996). Fruit set for pollinators that are diurnal (birds and bees) versus nocturnal (bats) for *C. gigantea* is 68% versus 40%. In contrast, species in the tropics are self-incompatible and are pollinated exclusively by bats (Sosa and Soriano 1992; Valiente-Banuet et al. 1996, 1997a,b; Nassar et al. 1997; Casas et al. 1999). This predictability in pollinator availability is lower in extratropical areas, where nectar-feeding bats are seasonal migrants from Arizona and northern Sonora to the tropical deciduous forests of Sonora and Sinaloa (Rojas-Martínez et al. 1999). In contrast, *Leptonycteris* spp. have resident populations within the tropics, e.g., in the Tehuacán Valley (Rojas-Martínez and Valiente-Banuet 1996; Rojas-Martínez et al. 1999), as explained by the predictability of pollinators throughout the year (Valiente-Banuet et al. 1997a,b; Rojas-Martínez et al. 1999). Anthesis for most columnar cacti lasts about 12 hours in the intertropical deserts of Venezuela, 13 to 15 hours in Mexico, and even longer (19–23 hours) for *C. gigantea, P. pringlei,*

and *S. thurberi* in the Sonoran Desert (Alcorn et al. 1961; McGregor et al. 1959, 1962; Fleming et al. 1996; Valiente-Banuet et al. 1996). An obligate pollination mutualism occurs for *Lophocereus schottii* and the moth *Upiga virescens* in the Sonoran Desert (Fleming and Holland 1998).

The cactus family is ideal for studying breeding-system evolution, because trioecy occurs for *P. pringlei* with males, seed-producing females, and hermaphrodites (Fleming et al. 1994), and androdioecy occurs for *Neobuxbaumia mezcalaensis* with male (female sterile) and hermaphrodite individual plants (Table 6.3; Valiente-Banuet et al. 1997a). Trioecy and androdioecy are uncommon sexual systems; androdioecy is uncommon because of the difficulty for male (female sterile) plants to invade hermaphrodite populations (Charlesworth and Charlesworth 1978). Other cactus species have dioecious or subdioecious breeding systems (i.e., with male or female sterile and hermaphrodite plants). Four species of *Opuntia* (*O. glausecens, O. grandis, O. robusta,* and *O. stenopetala*) are dioecious, two species of *Mammillaria* are dioecious (*M. dioica* and *M. neopalmeri*), and *Selenicereus innesii* is gynodioecious (Parfitt 1985; Del Castillo 1986; Hoffman 1992).

Seed Dispersal

Seed dispersal is an important stage in the life cycle of cacti; it can favor the success of seeds under the canopies of nurse plants (Valiente-Banuet and Ezcurra 1991; Godínez-Alvarez et al. 1999). The successful dispersal of seeds to these sites can increase the area of distribution of cacti and affects gene flow among populations (Howe and Smallwood 1982). Information about the mechanisms by which cactus seeds are dispersed under natural conditions is scarce. In this regard, Bregman (1988), analyzing the structural characteristics of fruits and seeds of more than 100 species of cacti, suggested that these plants can be dispersed by wind (anemochory), water (hydrochory), and animals (zoochory).

Of possible mechanisms of seed dispersal, anemochory and hydrochory are less studied. Anemochory has been suggested for individuals of the genus *Pterocactus,* which present dry fruits with winged seeds that are exposed when the fruit dehisce at maturity (Bregman 1988). Hydrochory has been suggested for seeds of the genera *Astrophytum, Discocactus, Frailea, Gymnocalycium, Matucana,* and *Thrixanthocereus.* These cacti produce dry fruit containing relatively large seeds with a large hilum, a thin seed coat, and a small embryo, which presumably favor the dispersal by water (Bregman 1988).

Zoochory is the most common mode of transportation of seeds reported for different species of cacti (Table 6.4). Bregman (1988) suggested that seed dispersal by animals occurred in three ways: (1) seeds could be transported passively on the outside of animals, epizoochory; (2) seeds could be transported externally by an animal, synzoochory; or (3) seeds could be consumed by animals, endozoochory. Epizoochory is found only in epiphytic cacti of the genus *Rhipsalis,* whose fruits contain sticky seeds that adhere to the bill of birds feeding on the fruits. Synzoochory has been suggested for cacti of the genera *Opuntia, Parodia, Blossfeldia, Krainzia, Strombocactus,* and *Aztekium,* among others. Seeds of these cacti are generally predated upon by harvester ants (*Pogonomyrmex* spp., *Messor* spp.); however, dispersal can also occur when the ants accidentally lose seeds during transportation to their nests (Vargas-Mendoza and González-Espinosa 1992).

Endozoochory occurs for species of cacti that produce fleshy fruits. This kind of fruit is found in most species in the genera *Opuntia, Epiphyllum, Hylocereus, Pachycereus, Ferocactus, Melocactus, Carnegiea, Neobuxbaumia, Myrtillocactus, Stenocereus, Cephalocereus, Subpilocereus,* and *Pilosocereus,* among others, and serves as an attractant to different groups of animals, such as reptiles, birds, and mammals that consume the pulp and seeds (Steenbergh and Lowe 1977; Silva 1988; Wendelken and Martin 1988; León de la Luz and Cadena 1991; Soriano et al. 1991; Vargas-Mendoza and González-Espinosa 1992; Cortes Figueira et al. 1994; Silvius 1995; Valiente-Banuet et al. 1996). Indeed, *Opuntia* fruit were probably consumed by extinct megafauna about 10,000 years ago (Janzen 1986).

In some cases, passage of seeds through vertebrate guts increases germination, such as for *Melocactus violaceus* (Cortes Figueira et al. 1994) and *Stenocereus gummosus* (León de la Luz and Cadena 1991), whereas for others, seed germination decreases or there is no effect, as for *C. gigantea* (Steenbergh and Lowe 1977), *Neobuxbaumia tetetzo* (H. Godínez-Alvarez, A. Rojas-Martínez, and A. Valiente-Banuet, unpublished observations), *Opuntia rastrera* (Mandujano et al. 1997), and *Stenocereus griseus* (Silvius 1995). The central questions for seed dispersal by animals are to determine if animal vectors are effective dispersers that transport seeds to safe sites beneath nurse plants and to establish whether seed dispersal has consequences on the maintenance of cactus populations under natural conditions. Vargas-Mendoza and González-Espinosa (1992) found that survival of seedlings of *Opuntia streptacantha* during the first 5 months differed among microsites. Birds and bats consume the fruits of *Neobuxbaumia tetetzo,* but bats more effectively disperse viable

TABLE 6.4
Seed dispersal by animals for cacti

Species	Seed dispersers	Reference
Carnegiea gigantea	Different species of insects, birds, and mammals	Steenbergh and Lowe (1977)
	Zenaida asiatica	Olin et al. (1989)
Melocactus violaceus	Lizards	Cortes Figueira et al. (1994)
Neobuxbaumia tetetzo	Different species of birds and bats	Valiente-Banuet et al. (1996); H. Godínez-Alvarez, A. Rojas-Martínez, and A. Valiente-Banuet (unpublished observations)
Opuntia rastrera	Different species of mammals and birds	Mandujano et al. (1997)
O. streptacantha	*Pogonomyrmex barbatus* and other species of rodents	Vargas-Mendoza and González-Espinosa (1992)
Pilosocereus maxonii	Birds (18 spp.)	Wendelken and Martin (1988)
P. tillianus	*Glossophaga longirotris*	Soriano et al. (1991)
Stenocereus eichlamii	Birds (18 spp.)	Wendelken and Mattin (1988)
S. griseus	*Glossophaga longirotris*	Soriano et al. (1991)
	Birds (14 spp.)	Silvius (1995)
S. gummosus	Different species of insects, reptiles, birds, and mammals	León de la Luz and Cadena (1991)
Subpilocereus repandus	*Glossophaga longirotris*	Soriano et al. (1991)

seeds to safe sites (H. Godínez-Alvarez, A. Rojas-Martínez, and A. Valiente-Banuet, unpublished observations).

Population Dynamics

The maintenance of cactus populations under natural conditions is affected by various interactions with other organisms as well as by abiotic factors, such as rainfall and solar radiation (Fig. 6.1). The assessment of the relative importance of each factor provides information on the main causes that affect the population dynamics of these plants. In this respect, matrix models are a useful tool to quantify the relative contribution made by different life stages to the rate of population increase. In such demographic models, individuals are grouped into size categories, and a projection matrix is constructed according to the survival, growth, and reproduction probabilities of the individuals in each category. This projection matrix is formed by three parts: (1) the first row includes the fecundity values for all of the reproductive classes, (2) the main diagonal includes the probabilities that individuals remain in the same size class after one year, and (3) the first lower subdiagonal incorporates the probabilities that individuals grow to the next size class after one year. The solution of this model permits one to obtain the rate of population increase (the largest positive eigenvalue), the stable size distribution (right eigenvector), and the reproductive values (left eigenvector; De Kroon et al. 1986). Moreover, elasticity can be analyzed for the critical stages of the life cycle. Elasticity is a relative measure, between 0 and 1 (or 0 and 100%), of the change in the rate of population increase in response to changes in matrix values (De Kroon et al. 1986).

Studies with this approach have been conducted with the giant columnar cacti *C. gigantea* (Silvertown et al. 1993), *Neobuxbaumia tetetzo* (Godínez-Alvarez et al. 1999), and *P. pringlei.* These studies show similar demographic patterns in which the survivorship of young individuals makes a higher contribution to the rate of population increase than does growth and reproduction of older plants (Fig. 6.1). The elasticity values of survivorship varies among species, from 86% for *P. pringlei,* 91% for *N. tetetzo,* to 99% for *C. gigantea* (Silvertown et al. 1993; Godínez-Alvarez et al. 1999).

Elasticity analyses of *N. tetetzo* and *P. pringlei* indicate that survivorship of immature and mature individuals have the highest values, ranging from 20 to 60% (Fig. 6.2). Survivorship of these categories is affected by competitive interactions with other plants of the same and/or different species (McAuliffe 1984b; McAuliffe and Janzen 1986; Valiente-Banuet et al. 1991b; Flores-Martínez et al. 1998). On the other hand, elasticity values for the rest of the cat-

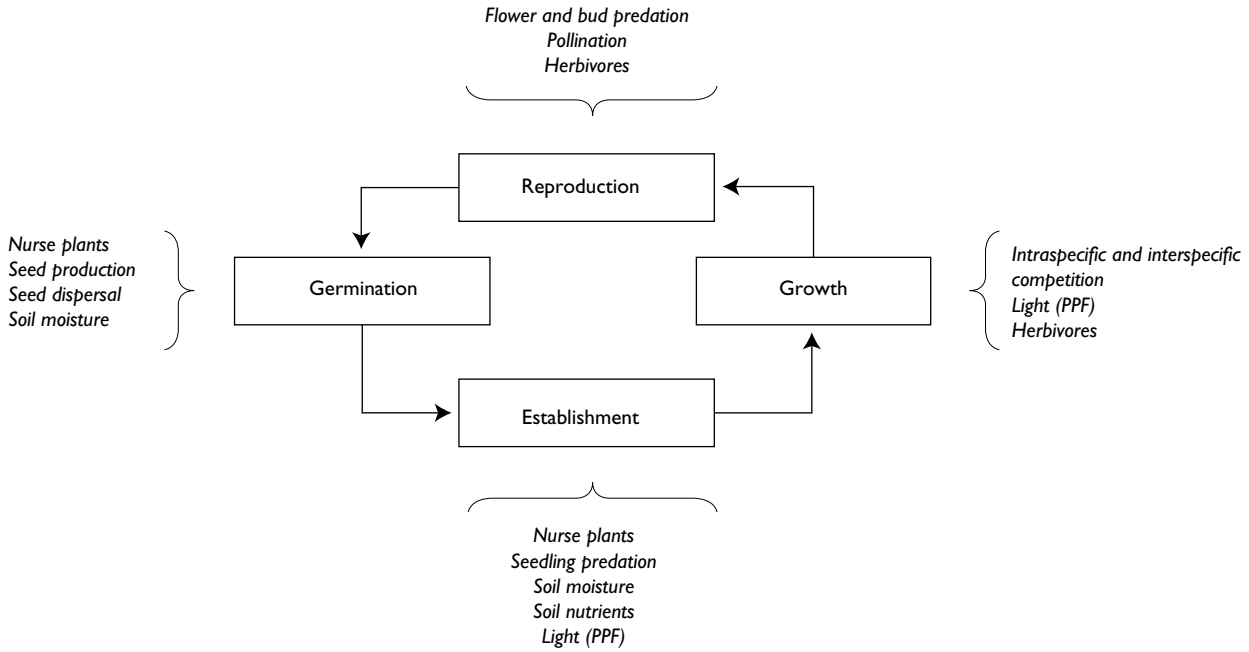


Figure 6.1. Biotic and abiotic factors affecting the life cycle of cacti.

egories for both species vary between 5 and 10% (Fig. 6.2). Although survivorship of *N. tetetzo* and *P. pringlei* seedlings does not have a high elasticity value (5%), this life cycle stage plays a significant role in the population dynamics because their survival probabilities are low and highly variable (6×10^{-4} in *N. tetetzo* after 2 years, Godínez-Alvarez et al. 1999; 0.01 in *P. pringlei* after 1 year, C. Silva-Pereyra, A. Valiente-Banuet, L. Valiente, P. Dávila, and J. Ortega, unpublished observations). The main mortality factor for seeds is predation by birds, rodents, and ants; for seedlings, desiccation by direct solar irradiation is the principal mortality factor. The survivorship pattern of these cacti indicates a high mortality for seeds and seedlings and greater survivorship for older individuals (a type III curve; Steenbergh and Lowe 1969; Valiente-Banuet and Ezcurra 1991). This survivorship pattern has also been found for other species of cacti, such as *Ferocactus acanthodes* (Jordan and Nobel 1981), *F. cylindraceus* (Bowers 1997), *Lophocereus schottii* (Parker 1989), *Mammillaria gaumeri* (Leirana-Alcocer and Parra-Tabla 1999), and *Stenocereus thurberi* (Parker 1987). Because the survivorship of seeds and seedlings depends on the arrival of seeds to sites under perennial plants (Fig. 6.1), the association of cacti with nurse plants is an important interaction in the population dynamics of cacti. The protection provided by nurse plants decreases the probability of mortality of seeds and seedlings, thereby increasing the probability that seedlings grow to maturity (Turner et al. 1966; Steenbergh and Lowe 1969, 1977; Valiente-Banuet and Ezcurra 1991).

Elasticity analyses of *N. tetetzo* and *P. pringlei* also indicate that seed dispersal is an important interaction in the population dynamics of cacti (Fig. 6.2). Frugivorous birds and bats consume the fleshy fruits of different species of cacti, such as *C. gigantea* (Steenbergh and Lowe 1977; Olin et al. 1989) and *N. tetetzo* (Valiente-Banuet et al. 1996). These fruit-eating animals can transport seeds directly to the canopies of nurse plants, affecting the population dynamics of these cacti. Bats are actually better dispersers than birds for *N. tetetzo,* because they transport intact and viable seeds directly to the nurse plants, thereby maintaning a continual flux of seeds to sites for seedling establishment.

Although demographic models indicate that biotic interactions are more significant than abiotic factors, soil evolution plays a major role in the population dynamics of *P. pringlei* (McAuliffe 1991; Valiente-Banuet et al. 1995a). In alluvial landscapes, cacti have their densest populations in young, coarse-textured soils (Parker 1989, 1995; McAuliffe 1991), with marginal populations in older alluvial soils that have higher per capita mortality than those in younger deposits. These observations suggest declines from what originally were denser populations (McAuliffe 1991). In alluvial regions, soils derive from the same source and usually share the same climatic conditions, but pedogenetic processes occur at different times, e.g., soils of alluvial fans and de-

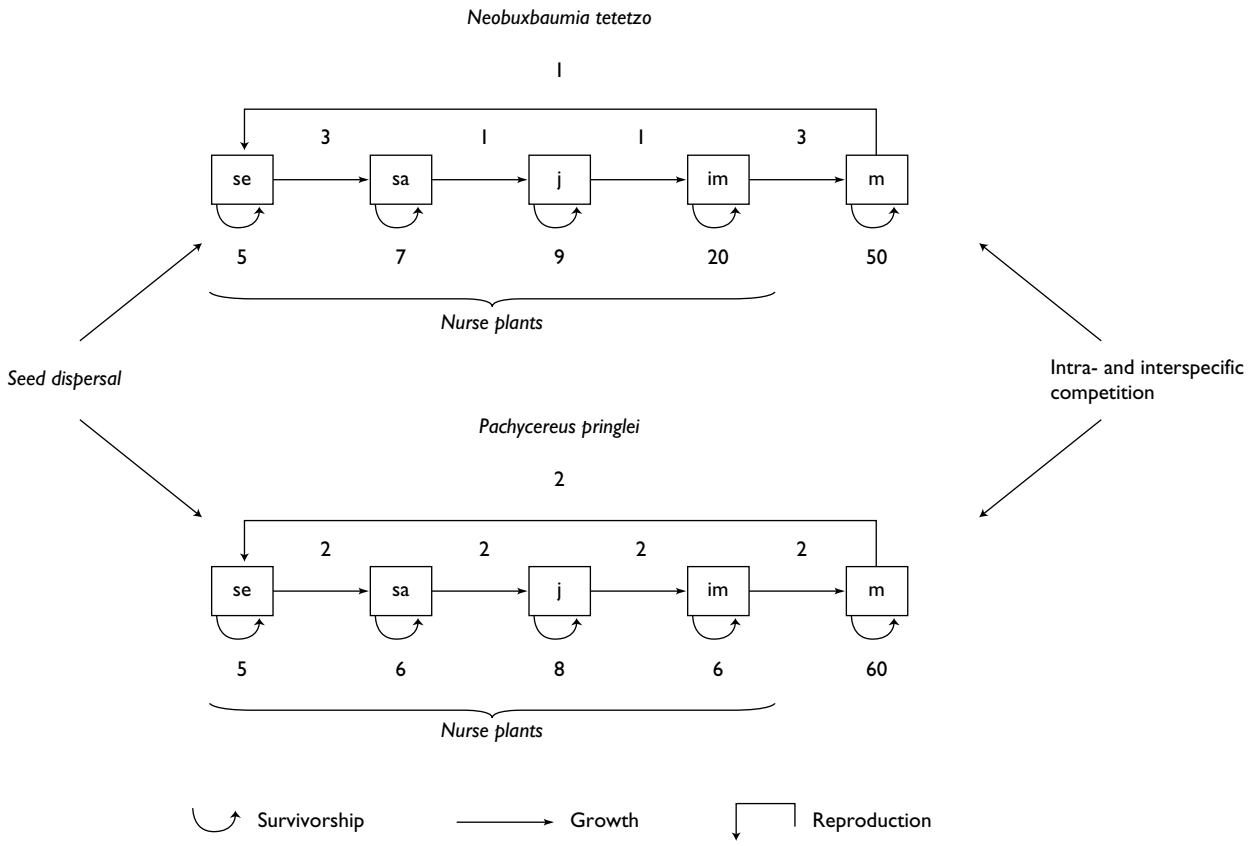


Figure. 6.2. Life-cycle diagram and elasticity values of two columnar cacti, *Neobuxbaumia tetetzo* and *Pachycereus pringlei.* Values are given in percentages. Se = seedlings (0–15 cm in height); sa = saplings (15–45 cm); j = juvenile (45–100 cm); im = immature (100–150 cm); m = mature (150–>650 cm). Values corresponding to seed germination and seedling establishment are incorportated in those for the reproduction of mature individuals. References: for *N. tetetzo,* Godínez-Alvarez et al. 1999; for *P. pringlei,* C. Silva-Pereyra, A. Valiente-Banuet, L. Valiente, J. Ortega-Ramírez, and P. Dávila, unpublished observations.

bris deposits become progressively more well developed over time (Webb et al. 1987; McAuliffe 1994; Parker 1995; Bowers 1997; Valiente-Banuet et al. 1995b). Older soils usually contain well developed argillic horizons and calcium carbonate ($CaCO_3$) accumulation in the Bk horizon, both reducing water availability (Hennesy et al. 1983). Thus cactus populations show different structures and composition among different-aged soils, leading to major differences in the population dynamics. For example, soil evolution for *P. pringlei* in Baja California Sur reduces seed production, seedling establishment, survival, and growth, and populations in younger-soil deposits have positive rates of increase (C. Silva-Pereyra, A. Valiente-Banuet, and J. Ortega, unpublished observations). This pattern has also been reported for other *P. pringlei* populations and for *Fouquieria columnaris* (McAuliffe 1991). In all cases, soil geomorphic development in alluvial landscapes is a key to spatial heterogeneity in plant population dynamics of cacti, leading to a metapopulation approach (Fig. 6.3).

To understand the population dynamics of cacti, a hierarchial organization of biotic and abiotic factors should be considered (Fig. 6.3). Biotic interactions may be the main factors that affect cacti at a local population level, whereas dispersion among populations and the effects of soil types on recruitment become important at the metapopulation level. Finally, the geomorphic history of the localities in which populations of cacti occur should be analyzed to understand population dynamics at the landscape level (Fig. 6.3).

Community Ecology

Cacti have great diversity in the Sonoran, Chihuahuan, and Tehuacán-Cuicatlán deserts. Due to the relative uniformity of deserts and the apparently stressful conditions imposed upon desert species, early studies that were mostly autoecological have dominated the discussion about how diversity is maintained (Noy-Meir 1973). However, since 1990 different studies have progressed toward an under-

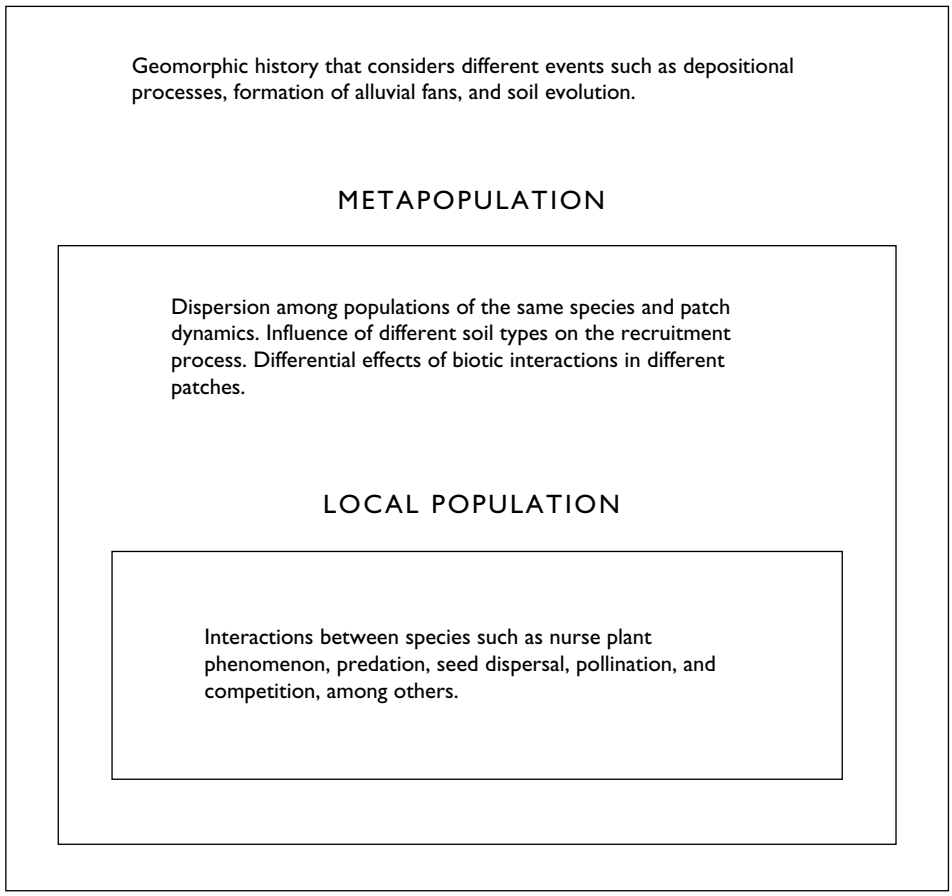

LANDSCAPE
Geomorphic history that considers different events such as depositional processes, formation of alluvial fans, and soil evolution.
METAPOPULATION
Dispersion among populations of the same species and patch dynamics. Influence of different soil types on the recruitment process. Differential effects of biotic interactions in different patches.
LOCAL POPULATION
Interactions between species such as nurse plant phenomenon, predation, seed dispersal, pollination, and competition, among others.

Figure 6.3. Hierarchical organization of biotic and abiotic factors affecting the population dynamics of cacti.

standing about the role of biotic interactions on species coexistence in addition to the analysis of abiotic conditions.

Cactus-dominated communities support a surprisingly diverse fauna and flora that include hundreds of species (Table 6.5). The classification systems of the vegetation of Mexico (Miranda and Hernández 1963; Rzedowski 1978) recognize different plant associations dominated by cacti: Nopaleras, mostly in the Chihuahuan and the Sonoran deserts, and "sarcocaulescent shrublands" including Cardonales, Tetecheras, and "Stenocerales" dominated by giant columnar cacti in the Tehuacán-Cuicatlán Valley, the southern part of the Chihuahuan Desert in Querétaro and Hidalgo, and the Sonoran Desert. Plant associations dominated by *Carnegiea gigantea* and *Pachycereus pringlei* occur in the Sonoran Desert (Turner et al. 1995). Indeed, *P. pringlei* is the most widely distributed dominant species in Baja California. In the Tehuacán-Cuicatlán Valley, a total of nine vegetation types are dominated by giant columnar cacti (Osorio et al. 1996). In these ecosystems, trees and shrubs, while modifying the microenvironmental conditions beneath their canopies, are controlling the availability of resources to other organisms by creating special habitats. Thus nurse-plant associations significantly contribute to the establishment of nearly all cactus species, acting as "ecosystem engineers" (Jones et al. 1997) and playing a major role in determining the structure and functioning of desert ecosystems (Valiente-Banuet and Ezcurra 1991).

Species can concentrate beneath the canopies of nurse plants—in some communities 60% of the species are found there (Valiente-Banuet 1991). This affects intraspecific competition, as for *Carnegiea gigantea* (McAuliffe and Janzen 1986), and interspecific competition (McAuliffe 1984; Valiente-Banuet et al. 1991b). Once a columnar cactus grows to more than 1 m in height, it may outcompete its nurse plant, defining a cyclical relationship in which the association starts as a facilitation process and

TABLE 6.5
Cactus-dominated ecosystems in Mexico and their species richness

Plant association	Locality	Dominant cacti	Species richness (number of plant species in 1,000 m^2 quadrats)				
			Plants	*Rodents*	*Bats*	*Birds*	*Reptiles*
Chihuahuan Desert Nopalera	Mapimí, Durango	*Opuntia rastrera, O. microdasys, O. violacea*	30	9	9	23	6
Neobuxbaumia tetetzo Tetechera	Tehuacán Valley, Puebla	*N. tetetzo, Myrtillocactus geometrizans*	46	4	34	91	—
Cephalocereus columna-trajani Cardonal	Tehuacán Valley, Puebla	*C. columna-trajani*	54	4	34	91	—
Stenocereus stellatus Cardonal	Tehuacán Valley, Puebla	*S. stellatus, S. pruinosus, Opuntia pilifera, Myrtillocactus geometrizans*	35	—	34	91	—
Pachycereus weberi Cardonal	Tehuacán Valley, Puebla	*P. weberi, Opuntia pilifera, O. puberula, Stenocereus pruinosus*	48	4	34	91	—
Escontria chiotilla Chiotillal	Tehuacán Valley, Puebla	*E. chiotilla, Stenocereus stellatus*	34	4	34	91	—
Mitrocereus fulviceps Cardonal	Tehuacán Valley, Puebla	*M. fulviceps, Echinocactus platyacanthus*	45	—	34	91	—
Pachycerus pringlei Cardonal	Sonoran Desert, Baja California Sur	*P. pringlei*	31	4	26	~60	—

Adapted from Barbault and Halffter (1981), Delhoume and Maury (1992), Arizmendi and Espinosa de los Monteros (1996), and Valiente-Banuet and Arizmendi (1998).

finishes as a competitive exclusion between the cactus and its perennial nurse plant (Yeaton 1978; McAuliffe 1988). Cyclical dynamics can be important in structuring desert communities, and the process has been defined as Markovian in community dynamics (McAuliffe 1988). Indeed, complex combinations of interactions are widespread in desert communities, and the balance between facilitation and competition, which varies with life stage, physiology, and environmental stresses, deserves further research (Valiente-Banuet and Ezcurra 1991; Bertness and Callaway 1994; Callaway and Walker 1997). For instance, the population dynamics of *P. pringlei* established in well-developed Pleistocene alluvial soils may drift toward extinction, especially during extended dry periods, whereas in young Holocene soils with more favorable moisture conditions, biotic interactions have a central role along its different life-cycle stages (C. Silva-Pereyra, A. Valiente-Banuet, L. Valiente, P. Dávila, and J. Ortega, unpublished observations).

Pollination and seed production are caused by a wide array of animal vectors, such as bees, hummingbirds, hawkmoths, and bats. In some high diversity areas, cacti maintain different and diverse guilds of cactus pollinators, such as about 90 species of bees that visit *Opuntia* flowers in the Chihuahuan Desert (Grant and Hurd 1979) and 9 species of nectar-feeding bats in the columnar cactus forests of south-central Mexico (Rojas-Martínez and Valiente-Banuet 1996; Valiente-Banuet et al. 1996).

The nectar-feeding bat *Leptonycteris curasoae* is a latitudinal migrant throughout its distribution in North America (Cockrum 1991; Fleming et al. 1993) and the most important pollinator of columnar cacti (Valiente-Banuet et al. 1996, 1997a,b). It has resident populations in the Tehuacán Valley and the Balsas River Basin (Rojas-Martínez et al. 1999), and its pollination relationships with columnar cacti are tight and coupled. In the northern limit of its distribution (southwestern United States), *L. curasoae* migrates during fall and winter, probably to the tropical deciduous forests of Sonora, Mexico, following the seasonal availability of floral resources (Rojas-Martínez et al. 1999). The predominance of cactus-floral resources during spring and summer in these ecosystems and during autumn and winter in tropical deciduous forests supports high population densities of nectar- and fruit-feeding bats (Rojas-Martínez and Valiente-Banuet 1996) and is correlated with the arrival of a great number of bird species that consume fruits and seeds (Arizmendi and Espinosa de los Monteros 1996). Indeed, bats play two important ecological roles by pollinating the flowers and dispersing the seeds directly to safe sites. Those biotic interactions that increase the average individual fitness of at least one species with no negative effects on any other species are defined as positive (Hacker and Gaines 1997). Positive biotic interactions apparently have the predominant effects on species diversity in such ecosystems. However, more research needs to be done in these environments to determine indirect effects of species.

Conclusions and Future Prospects

At the population level, biotic interactions that cacti have within and between trophic levels help determine survivorship, mortality, and fecundity patterns observed under natural conditions. Although demographic models indicate that positive interactions (i.e., facilitation) affect the most sensitive life-cycle stages, the contribution of biotic and abiotic factors to the population dynamics of a particular cactus species is poorly understood. Much research needs to be done to analyze the importance of a metapopulation approach in which soils occupy a central role (Fig. 6.3). Specifically, soil-geomorphic evolution is a key aspect for evaluating the relative importance of abiotic components versus biotic interactions on demography. Preliminary analyses indicate that soil evolution exerts a strong influence on the predominance of cacti in arid environments.

At the community level, biotic interactions also occupy a central role in the explanation of how species coexistence is maintained. Positive interactions such as nurse-plant associations, pollination mutualisms, and seed dispersal strategies clearly suggest that biotic interactions contribute to species maintenance. However, indirect interactions have received little research attention, and almost all investigations have addressed the role of pairwise interactions on particular species. As multispecies systems, cactus-dominated communities deserve research on top-down processes that consider the role of predators in regulating competitive effects among plants. Moreover, considering the extremely important structural dominance of cacti and the trophic relationships between these plants and animals, bottom-up effects have been suggested but have never been properly analyzed.

Considering the economic, cultural, and religious importance of cacti in Mexico, understanding the factors that control the abundance and distribution of cacti over arid landscapes should be a major objective of ecological investigations in deserts. The information presented indicates that many aspects need to be considered to have a more comprehensive knowledge about how to conserve and to manage this highly diversified group of plants (Chapter 8). Indeed, the protection of positive interactions

should be a high priority for maintaining these plants in their natural environments.

Acknowledgments

The authors thank Fondo Mexicano para la Conservación de la Naturaleza (Project A1–97/36), Dirección General de Asuntos del Personal Académico (Project DGAPA-IN-207798), and Instituto de Ecología UNAM for supporting our studies and María del Coro Arizmendi for comments on the manuscript. A.V.-B. dedicates this chapter to the memory of Dr. Carlos Vázquez-Yanes.

Literature Cited

Alcorn, S. M., S. E. McGregor, and G. Olin. 1961. Pollination of Saguaro cactus by doves, nectar-feeding bats and honey bees. *Science* 132: 1594–1595.

Alcorn, S. M., S. E. McGregor, and G. Olin. 1962. Pollination requirements of the Organpipe cactus. *Cactus and Succulent Journal (U.S.)* 34: 134–138.

Altesor, A., E. Ezcurra, and C. Silva. 1992. Changes in the photosynthetic metabolism during the early ontogeny of four cactus species. *Acta Oecologica* 13: 777–785.

Arias, S. 1993. Cactáceas: Conservación y diversidad en México. *Revista Mexicana de Historia Natural* 44: 109–115.

Arizmendi, M. C., and A. Espinosa de los Monteros. 1996. Avifauna de los bosques de cactáceas columnares en el Valle de Tehuacán. *Acta Zoológica Mexicana* (n.s.) 67: 25–46.

Arriaga, L., Y. Maya, S. Diaz, and J. Cancino. 1993. Association between cacti and nurse perennials in a heterogeneous tropical dry forest in northwestern Mexico. *Journal of Vegetation Science* 4: 349–356.

Barbault, R., and G. Halffter. 1981. *Ecology of the Chihuahuan Desert.* Instituto de Ecología, Jalapa, Mexico.

Barthlott, W., and D. R. Hunt. 1993. Cactaceae. In *The Families and Genera of Vascular Plants. Vol. III, Flowering Plants, Dicotyledons* (K. Kubitzk, J. G. Rohwer, and V. Bittrich, eds.). Springer-Verlag, Berlin. Pp. 161–197.

Bertness, M. D., and R. M. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191–193.

Bowers, J. E. 1997. Demographic patterns of *Ferocactus cylindraceus* in relation to substrate age and grazing history. *Plant Ecology* 133: 37–48.

Bravo-Hollis, H. 1978. *Las Cactáceas de México,* Vol. 1, 2nd ed. Universidad Nacional Autónoma de México, Mexico City.

Bregman, R. 1988. Forms of seed dispersal in Cactaceae. *Acta Botanica Neerlandica* 37: 395–402.

Brum, G. D. 1973. Ecology of the saguaro (*Carnegiea gigantea*): Phenology and establishment in marginal populations. *Madroño* 22: 195–204.

Callaway, R. M., and L. H. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology* 78: 1958–1965.

Casas, A., A. Valiente-Banuet, A. Rojas-Martínez, and P. Dávila. 1999. Reproductive biology and the process of domestication of the columnar cactus *Stenocereus stellatus* in central Mexico. *American Journal of Botany* 86: 534–542.

Charlesworth, B., and D. Charlesworth. 1978. A model for the evolution of dioecy and gynodioecy. *American Naturalist* 112: 975–977.

Cockrum, E. L. 1991. Seasonal distribution of northwestern populations of the long nosed bats family Phyllostomidae. *Anales del Instituto de Biología. Serie Zoología* 62: 181–202.

Cortes-Figueira, J. E., J. Vasconcellos-Neto, M. A. García, and A. L. Teixeira de Souza. 1994. Saurocory in *Melocactus violaceus* (Cactaceae). *Biotropica* 26: 295–301.

De Kroon, H., A. Plaiser, J. van Groenendael, and H. Caswell. 1986. Elasticity: The relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427–1431.

Del Castillo, R. F. 1986. La selección natural de los sistemas de cruzamiento en *Opuntia robusta.* Master's Thesis, Colegio de Postgraduados, Chapingo, Mexico.

Delhoume, J. P., and M. E. Maury. 1992. *Actas del Seminario Mapimí.* Instituto de Ecología, Mexico City.

De Viana, M. L. 1997. Distribución espacial de *Trichocereus pasacana* (Cactaceae) en relación al espacio disponible y al banco de semillas. *Revista de Biología Tropical* 44: 95–103.

Dubrovsky, J. G. 1996. Seed hydration memory in Sonoran Desert cacti and its ecological implication. *American Journal of Botany* 83: 624–632.

Dubrovsky, J. G. 1998. Discontinuous hydration as a facultative requirement for seed germination in two cactus species of the Sonoran Desert. *Journal of the Torrey Botanical Society* 125: 33–39.

Faegri, K., and L. van der Pijl. 1979. *The Principles of*

Pollination Ecology, 3rd rev. ed. Pergamon Press, Oxford.

Fleming, T. H., R. A. Núñez, and S. L. da S. Lobo. 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon isotope analysis. *Oecologia* 94: 72–75.

Fleming, T. H., S. Maurice, S. L. Buchmann, and M. D. Tuttle. 1994. Reproductive biology and relative male and female fitness in a trioecious cactus, *Pachycereus pringlei* (Cactaceae). *American Journal of Botany* 81: 858–867.

Fleming, T. H.., M. D. Tuttle, and M. A. Horner. 1996. Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran Desert columnar cacti. *The Southwestern Naturalist* 41: 257–269.

Fleming, T. H., and J. N. Holland. 1998. The evolution of obligate pollination mutualisms: Senita cactus and senita moth. *Oecologia* 114: 368–375.

Flores-Martínez, A., E. Ezcurra, and S. Sánchez-Colón. 1998. Water availability and the competitive effect of a columnar cactus on its nurse plant. *Acta Oecologica* 19: 1–8.

Franco, A. C., and P. S. Nobel. 1989. Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* 77: 870–886.

García-Moya, E., and C. M. McKell. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51: 81–88.

Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer.* Harvard University Press, Cambridge, Massachusetts.

Godínez-Alvarez, H., and A. Valiente-Banuet. 1998. Germination and early seedling growth of Tehuacan Valley cacti species: The role of soils and seed ingestion by dispersers on seedling growth. *Journal of Arid Environments* 39: 21–31.

Godínez-Alvarez, H., A. Valiente-Banuet, and B. L. Valiente. 1999. Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley, Mexico. *Canadian Journal of Botany* 77: 203–208.

Grant, V., and K. A. Grant. 1979. The pollination spectrum in the southwestern American cactus flora. *Plant Systematics and Evolution* 133: 29–37.

Grant, V., and P. D. Hurd. 1979. Pollination of the southwestern Opuntias. *Plant Systematics and Evolution* 133: 15–28.

Hacker, S. D., and S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78: 1990–2003.

Hennesy, J. T., R. P. Gibbens, J. M. Tromble, and M. Cardenas. 1983. Water properties of caliche. *Journal of Range Management* 36: 723–726.

Hoffman, M. T. 1992. Functional dioecy in *Echinocereus coccineus* (Cactaceae): Breeding system, sex ratios and geographical range of sexual dimorphism. *American Journal of Botany* 79: 1382–1388.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

Hutto, R. L., J. R. McAuliffe, and L. Hogan. 1986. Distributional associates of the saguaro (*Carnegiea gigantea*). *The Southwestern Naturalist* 31: 469–476.

Janzen, D. H. 1986. Chihuahuan Desert nopaleras: Defaunated big mammal vegetation. *Annual Review of Ecology and Systematics* 17: 595–636.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–1957.

Jordan, P. W., and P. S. Nobel. 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. *Ecology* 62: 901–906.

Kigel, J. 1995. Seed germination in arid and semi-arid regions. In *Seed Development and Germination* (J. Kigel and G. Galili, eds.). Marcel Dekker, New York. Pp. 645–699.

Leirana-Alcocer, J., and V. Parra-Tabla. 1999. Factors affecting the distribution, abundance and seedling survival of *Mammillaria gaumeri,* an endemic cactus of coastal Yucatán, México. *Journal of Arid Environments* 41: 421–428.

León de la Luz, J. L., and R. D. Cadena. 1991. Evaluación de la reproducción por semilla de la pitaya agria (*Stenocereus gummosus*) en Baja California Sur, México. *Acta Botánica Mexicana* 14: 75–87.

Mandujano, M. del C., J. Golubov, and C. Montaña. 1997. Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the southern Chihuahuan Desert. *Journal of Arid Environments* 36: 259–266.

McAuliffe, J. R. 1984a. Prey refugia and the distributions of two Sonoran Desert cacti. *Oecologia* 65: 82–85.

McAuliffe, J. R. 1984b. Sahuaro-nurse tree associations in the Sonoran Desert: Competitive effects of sahuaros. *Oecologia* 64: 319–321.

McAuliffe, J. R., and F. J. Janzen. 1986. Effects of intraspecific crowding on water uptake, water storage, apical growth, and reproductive potential in the sahuaro cactus, *Carnegiea gigantea. Botanical Gazette* 147: 334–341.

McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert plant communities. *The American Naturalist* 131: 459–490.

McAuliffe, J. R. 1991. Demographic shifts and plant succession along a late Holocene soil chronosequence in the Sonoran Desert of Baja California. *Journal of Arid Environments* 20: 165–178.

McAuliffe, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs* 64: 111–148.

McGregor, S. C., S. M. Alcorn, E. B. Kurtz, and G. D. Butler. 1959. Bee visitors to saguaro flowers. *Journal of Economic Entomology* 52: 1002–1004.

McGregor, S. C., S. M. Alcorn, E. B. Kurtz, and G. Olin. 1962. Pollination and pollinating agents of the saguaro. *Ecology* 43: 259–267.

Miranda, F., and E. X. Hernández. 1963. Los tipos de vegetación de México y su clasificación. *Boletín de la Sociedad Botánica de México* 28: 29–179.

Nassar, J. M., N. Ramírez, and O. Linares. 1997. Comparative pollination biology of Venezuelan columnar cacti and the role of nectar feeding bats in their sexual reproduction. *American Journal of Botany* 84: 918–927.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nolasco, H., F. Vega-Villasante, H. L. Romero-Schmidt, and A. Díaz-Rondero. 1996. The effects of salinity, acidity, light and temperature on the germination of seeds of cardón (*Pachycereus pringlei* (S. Wats.) Britton and Rose, Cactaceae). *Journal of Arid Environments* 33: 87–94.

Nolasco, H., F. Vega-Villasante, and A. Díaz-Rondero. 1997. Seed germination of *Stenocereus thurberi* (Cactaceae) under different solar irradiation levels. *Journal of Arid Environments* 36: 123–132.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 5: 25–51.

Olin, G., S. M. Alcorn, and J. M. Alcorn. 1989. Dispersal of viable saguaro seeds by white-winged doves (*Zenaida asiatica*). *The Southwestern Naturalist* 34: 282–284.

Osorio, B. O., A. Valiente-Banuet, P. Dávila, and R. Medina. 1996. Tipos de vegetación y diversidad β en el Valle de Zapotitlán de las Salinas, Puebla, México. *Boletín de la Sociedad Botánica de México* 59: 35–58.

Parfitt, B. D. 1985. Dioecy in North American Cactaceae: A review. *Sida* 11: 200–206.

Parker, K. C. 1987. Site-related demographic patterns of organ pipe cactus populations in southern Arizona. *Bulletin of the Torrey Botanical Club* 114: 149–155.

Parker, K. C. 1989. Height structure and reproductive characteristics of senita, *Lophocereus schottii* (Cactaceae), in southern Arizona. *The Southwestern Naturalist* 34: 392–401.

Parker, K. C. 1993. Climatic effects on regeneration trends for two columnar cacti in the northern Sonoran Desert. *Annals of the Association of American Geographers* 83: 452–474.

Parker, K. C. 1995. Effects of complex geomorphic history on soil and vegetation patterns on arid alluvial fans. *Journal of Arid Environments* 30: 19–39.

Petit, S. 1995. The pollinators of two species of columnar cacti on Curaçao, Netherlands Antilles. *Biotropica* 27: 538–541.

Porsch, O. 1939. Das Bestäubungsleben der Kakteenblüte, II. Cactaceae. *Jahrbuch der Deutsche Kakteen-Gesellschaft* II: 81–142.

Rojas-Aréchiga, M., A. Orozco-Segovia, and C. Vázquez-Yanes. 1997. Effect of light on the germination of seven species of cacti from the Zapotitlán Valley in Puebla, México. *Journal of Arid Environments* 36: 571–578.

Rojas-Aréchiga, M., C. Vázquez-Yanes, and A. Orozco-Segovia. 1998. Seed response to temperature of Mexican cacti species from two life forms: An ecophysiological interpretation. *Plant Ecology* 135: 207–214.

Rojas-Aréchiga, M., and C. Vázquez-Yanes. 2000. Cactus seed germination: A review. *Journal of Arid Environments* 44: 85–104.

Rojas-Martínez, A., and A. Valiente-Banuet. 1996. Análisis comparativo de la quiropterofauna del Valle de Tehuacán-Cuicatlán, Puebla-Oaxaca. *Acta Zoológica Mexicana* (n.s.) 67: 1–22.

Rojas-Martínez, A., A. Valiente-Banuet, Ma. Del C. Arizmendi, A. Alcántara-Egúren, and H. Arita. 1999. Seasonal distribution of the long-nosed bat (*Leptonycteris curasoae*) in North America: Does a generalized migration pattern really exist? *Journal of Biogeography* 26: 1065–1078.

Rzedowski, J. 1978. *Vegetación de México.* Editoral Limusa, Mexico City.

Sahley, C. T. 1996. Bat and hummingbird pollination of an autotetraploid columnar cactus, *Weberbaurocereus weberbaueri* (Cactaceae). *American Journal of Botany* 83: 1329–1336.

Shreve, F. 1951. *Vegetation and Flora of the Sonoran Desert,* Vol. 1. Carnegie Institution of Washington, Washington, D.C.

Silva, W. R. 1988. Ornitocoria em *Cereus peruvianus* (Cactaceae) na Serra do Japi, Estado de São Paulo. *Revista Brasileira de Biologia* 48: 381–389.

Silvertown, J. W., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81: 465–476.

Silvius, K. M. 1995. Avian consumers of cardón fruits (*Stenocereus griseus:* Cactaceae) on Margarita Island, Venezuela. *Biotropica* 27: 96–105.

Soriano, P. J., M. Sosa, and O. Rossell. 1991. Hábitos alimentarios de *Glossophaga longirostris* Miller (Chiroptera: Phyllostomidae) en una zona árida de los Andes venezolanos. *Revista de Biología Tropical* 39: 263–268.

Sosa, M., and P. Soriano. 1992. Los murciélagos y los cactus: una relación muy estrecha. *Carta Ecológica* 61: 7–10.

Steenbergh, W. H., and C. H. Lowe. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at the Saguaro National Monument, Arizona. *Ecology* 50: 825–834.

Steenbergh, W. H., and C. H. Lowe. 1977. *Ecology of the Saguaro. II. Reproduction, Germination, Establishment, Growth and Survival of the Young Plant.* National Park Service Scientific Monograph Series No. 8, U.S. Government Printing Office, Washington, D.C.

Suzán, H., G. Nabhan, and D. T. Patten. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. *Journal of Vegetation Science* 7: 635–644.

Turner, R. M., S. Alcorn, G. Olin, and J. A. Booth. 1966. The influence of shade, soil and water on saguaro seedling establishment. *Botanical Gazette* 127: 95–102.

Turner, R. M., J. E. Bowers, and T. L. Burgess. 1995. *Sonoran Desert Plants: An Ecological Atlas.* University of Arizona Press, Tucson.

Valiente-Banuet, A. 1991. Dinámica del establecimiento de cactáceas: patrones generales y consecuencias de los procesos de facilitación por plantas nodrizas en desiertos. Ph.D. Thesis, Universidad Nacional Autónoma de México, Mexico City.

Valiente-Banuet, A., O. Briones, A. Bolongaro-Crevenna, E. Ezcurra, M. Rosas, H. Núñez, G. Barnard, and E. Vázquez. 1991a. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science* 2: 15–20.

Valiente-Banuet, A., F. Vite, and A. Zavala-Hurtado. 1991b. Interaction between the cactus *Neobuxbaumia tetetzo* and the shrub *Mimosa luisana. Journal of Vegetation Science* 2: 11–14.

Valiente-Banuet, A., and E. Ezcurra. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology* 79: 961–971.

Valiente-Banuet, A., P. Dávila, M. C. Arizmendi, A. Rojas-Martínez, and A. Casas. 1995a. Bases ecológicas del desarrollo sustentable en zonas áridas: el caso de los bosques de cactáceas columnares en el Valle de Tehuacán y Baja California Sur, México. In *IV Curso sobre Desertificación y Desarrollo Sustentable en América Latina y el Caribe* (G. M. Anaya and C. S. F. Díaz, eds.). PNUMA-FAO, Mexico City. Pp. 20–36.

Valiente-Banuet, A., P. Dávila, R. J. Ortega, M. C. Arizmendi, J. L. León, A. Breceda, J. Cancino. 1995b. Influencia de la evolución de una pendiente de piedemonte en una vegetación de cardonal de *Pachycereus pringlei* en Baja California Sur, México. *Investigaciones Geográficas* 3: 101–113.

Valiente-Banuet, A., M. C. Arizmendi, A. Rojas-Martínez, and L. Domínguez-Canseco. 1996. Ecological relationships between columnar cacti and nectar feeding bats in Mexico. *Journal of Tropical Ecology* 12: 103–119.

Valiente-Banuet, A., A. Rojas-Martínez, M. C. Arizmendi, and P. Dávila. 1997a. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. *American Journal of Botany* 84: 452–455.

Valiente-Banuet, A., A. Rojas-Martínez, A. Casas, M. C. Arizmendi, and P. Dávila. 1997b. Pollination biology of two-winter-blooming giant columnar cacti in the Tehuacan Valley, central Mexico. *Journal of Arid Environments* 37: 331–341.

Valiente-Banuet, A., and M. C. Arizmendi. 1998. El escenario ecológico del Valle de Tehuacán-Cuicatlán. In *Tehuacan, Horizonte del Tiempo.* Club Rotario Tehuacán Manantiales, Mexico City. Pp. 45–61.

Vargas-Mendoza, M. C., and M. González-Espinosa. 1992. Habitat heterogeneity and seed dispersal of *Opuntia streptacantha* (Cactaceae) in nopaleras of central Mexico. *The Southwestern Naturalist* 37: 379–385.

Webb, R. H., J. W. Steiger, and R. M. Turner. 1987. Dynamics of Mojave desert shrub assemblages in the Panamint Mountains, California. *Ecology* 68: 478–490.

Wendelken, P. W., and R. F. Martin. 1988. Avian consumption of the fruit of the cacti *Stenocereus eichlamii* and *Pilosocereus maxonii* in Guatemala. *The American Midland Naturalist* 119: 235–243.

Yeaton, I. R. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. *Journal of Ecology* 66: 651–656.

CHAPTER

› 7 ‹

CONSUMPTION OF PLATYOPUNTIAS BY WILD VERTEBRATES

Eric Mellink and Mónica E. Riojas-López

Introduction
Consumption of Vegetative Structures
Cladode Preferences
Seasonal Effects for Herbivory
Nutritional Qualitites of Cladodes
Spine Effects on Herbivory
Consumption of Reproductive Structures
Flower Consumption
Fruit Consumption
Evolutionary and Ecological Context
Past and Present Herbivory Pressures
Galápagos Islands
Alienized Relations
Concluding Remarks
Literature Cited

Introduction

In arid lands, platyopuntias (prickly pear cacti, also called *nopales* [singular, *nopal*]) often appear as lush, exhuberant forage and, during the proper time of the year, bear brightly colored fruits, which, as Gibson and Nobel (1986) indicate, "would be a welcome waterhole and restaurant for animals." Cladodes and fruits of platyopuntias are indeed consumed by a variety of vertebrates in ways that affect entire ecosystems (Anthony 1954; Janzen 1986).

This chapter presents an overview of the utilization of platyopuntias by wild vertebrates. It also includes a list of the vertebrate species reported to be consumers of platyopuntias. Certainly this list is not complete, as many consumers have not been reported in the formal literature. Because of the natural distribution of platyopuntias, the information about vertebrate consumption is biased toward the deserts of North America and the Galápagos Islands. Most sources indicating consumption of platyopuntias by vertebrates present rather incidental information on the issue; only a few, notably those for the Galápagos Islands, derive from the study of ecological relations involving platyopuntias. Eighty-nine vertebrate species appear in the literature as consumers of platyopuntias: 9 species of reptiles, 26 of birds, and 54 of mammals (Table 7.1). Pads (cladodes) and fruits are the parts most often reported as consumed, although reports on the use of fruits may mask the use of seeds.

TABLE 7.1
A summary of wild, opuntiofagous vertebrates

Species	Part(s) consumed	Reference(s)
	Reptiles	
Berlandier's tortoise (*Gopherus berlandieri*)	Pads, petals, fruits	Auffenberg and Weaver (1969); Rose and Judd (1982)
Galápagos tortoise (*Testudo elephantinus*)	Pads, fruits	Thorton (1971); Biggs (1990)
Leopard tortoise (*Geochelone pardalis*)	Fruits	Milton (1992)
Galápagos land iguana (*Conocephalus pallidus*)	Pads, petals, fruits	Christian et al. (1984)
Galápagos land iguana (*C. subcristatus*)	Pads, petals	Thorton (1971); Biggs (1990)
Daphne lava lizard (*Microlophus albemarensis*)	Petals, nectar, pollen	East (1995)
Pinta lava lizard (*M. pacificus*)	Petals, nectar, pollen, fruits	Schluter (1984)
Whiptail (*Cnemidophorus lemniscatus*)	Petals	Mijares-Urrutia et al. (1997)
Lagarto Tizón (*Gallotia galloti*)	Fruits	Valido and Nogales (1994)
	Birds	
Ostrich (*Struthio camelus*)	Fruits	Burt-Davy (1920)
Emu (*Dromiceus* sp.)	Fruits	Darnell-Smith (1919)
Wild turkey (*Meleagris gallopavo*)	Fruits	Lehman (1984)
Scaled quail (*Callipepla squamata*)	Fruits	Lehman (1984); Brown (1989)
Northern bobwhite (*Colinus virginianus*)	Seeds	Lehman (1984)
White-winged dove (*Zenaida asiatica*)	Fruits	Lehman (1984); Gonzalez-Espinoza and Quintana-Ascencio (1986)
Galápagos dove (*Z. galapagoensis*)	Pads, petals, nectar, pollen, fruits, seeds	Grant and Grant (1979, 1981)
Mourning dove (*Z. macroura*)	Fruits	Lehman (1984)
Greater roadrunner (*Geococcyx californianus*)	Fruits	Clements and Shelford (1939)
Northern flicker (*Colaptes auratus*)	Fruits	Clements and Shelford (1939); Gonzalez-Espinoza and Quintana-Ascencio (1986)
Mexican jay (*Aphelocoma ultramarina*)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Black magpie (*Gymnorhina tibicen*)	Fruits	Darnell-Smith (1919)
Common raven (*Corvus corax*)	Fruits	M. Riojas-López (unpublished observations)
Chihuahuan raven (*C. cryptoleucus*)	Fruits	Lehman (1984); Gonzalez-Espinoza and Quintana-Ascencio (1986)
Little raven (*C. mellori*)	Fruits	McCulloch (1980)
Curve-billed thrasher (*Toxostoma curvirostre*)	Fruits	Lehman (1984); Gonzalez-Espinoza and Quintana-Ascencio (1986)
Galápagos mockingbird (*Nesomimus parvulus*)	Pads, nectar, pollen, seeds	Grant and Grant (1981)
Canyon towhee (*Pipilo fuscus*)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
House finch (*Carpodacus mexicanus*)	Fruits	"
Genovesa cactus finch (*Geospiza conirostris*)	Pads, nectar, pollen, seeds	Grant and Grant (1981, 1989)
Galápagos finch (*G. difficilis*)	Nectar, pollen, seeds	Bowman (1961); Grant and Grant (1981)
Daphne Major ground finch (*G. fortis*)	Nectar, pollen, seeds	Grant and Grant (1981); Price (1987); Grant (1996)
Galápagos finch (*G. fuliginosa*)	Nectar, pollen, seeds	Grant and Grant (1981); Dodd and Brady (1988)
Galápagos finch (*G. magnirostris*)	Nectar, pollen, seeds	Grant and Grant (1981)
Daphne Major cactus finch (*G. scandens*)	Pads, nectar, pollen, fruits, seeds	Lack (1947); Bowman (1961); Grant and Grant (1981); Millington and Grant (1983); Grant (1996)

TABLE 7.1 *(continued)*

Species	Part(s) consumed	Reference
	Mammals	
Mexican long-tongued bat (*Choeronycteris mexicana*)	Nectar, pollen	Dalquest (1953)
Big long-nosed bat (*Leptonycteris nivalis*)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Baboon (*Papio hamadryas*)	Fruits	Weed Section (1940)
"Monkeys" (Family Cercopithecidae)	Fruits	Weed Section (1940)
Shasta ground sloth (*Nothrotheriops shastense*)	Pads, petals, fruits	Long et al. (1974); Hansen (1978); Spaulding and Martin (1979)
European rabbit (*Oryctolagus cuniculus*)	Fruits	Darnell-Smith (1919)
Desert cottontail (*Sylvilagus audubonii*)	Pads, fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986); Hoffman et al. (1993)
Nuttall's cottontail (*S. nuttallii*)	Pads	MacCracken and Hansen (1984)
Antelope jackrabbit (*Lepus alleni*)	Pads	Vorhies and Taylor (1933)
Black-tailed jackrabbit (*L. californicus*)	Stems, pads, fruits	Vorhies and Taylor (1933); Timmons (1942); Riegel (1941); MacCracken and Hansen (1984); Hoffmeister (1986); Hoffman et al. (1993); E. Mellink and M. Riojas-López (unpublished observations)
White-tailed jackrabbit (*L. townsendii*)	Pads	Bear and Hansen (1966); Flinders and Hansen (1972), cited in Dunn et al. (1982)
Harris' antelope-squirrel (*Ammospermophilus harrisii*)	Fruits, seeds	Hoffmeister (1986)
Spotted ground squirrel (*Spermophilus spilosoma*)	Pads	Bailey (1931)
Thirteen-lined ground squirrel (*S. tridecemlineatus*)	Fruits, seeds	Riegel (1941); Lehman (1984)
Rock squirrel (*S. variegatus*)	Fruits	Hoffmeister (1986)
Ground squirrel (*S.* sp.)	Seeds	Janzen (1986)
Botta's pocket gopher (*Thomomys bottae*)	Roots, stems	Hoffmeister (1986)
Mountain pocket gopher (*T. talpoides*)	Pads	Vaughan (1967)
Baileyi's pocket mouse (*Chaetodipus baileyi*)	Seeds	Hoffmeister (1986)
Hispid pocket mouse (*C. hispidus*)	Seeds	Blair (1937)
Nelson's pocket mouse (*C. nelsoni*)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Southern banner-tailed kangaroo rat (*Dipodomys phillipsii*)	Fruits	"
Banner-tailed kangaroo rat (*D. spectabilis*)	Pads	Vorhies and Taylor (1922)
Mexican spiny pocket mouse (*Liomys irroratus*)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Galápagos rice rat (*Oryzomys galapagoensis*)	Seeds	Thorton (1971)
Rock mouse (*Peromyscus difficilis*)	Fruits	Dalquest (1953)
Pinyon mouse (*P. truei*)	Fruits	"
Deer mouse (*P.* sp.)	Seeds	Janzen (1986)
Hispid cotton rat (*Sigmodon hispidus*)	Pads	Lehman (1984)
White-throated packrat (*Neotoma albigula*)	Pads, fruits	Vorhies and Taylor (1940); Dalquest (1953); Gonzalez-Espinoza and Quintana-Ascencio (1986); Rangel and Mellink (1993)
Goldman's packrat (*N. goldmani*)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Desert packrat (*N. lepida*)	Pads	Hoffmeister (1986)
Black rat (*Rattus rattus*)	Seeds	Eliasson (1968)
North American porcupine (*Erethizon dorsatum*)	Fruits	Hoffmeister (1986)
Coyote (*Canis latrans*)	Fruits	Lehman (1984); Gonzalez-Espinoza and Quintana-Ascencio (1986); McLure et al. (1995)
Gray fox (*Urocyon cinereoargenteus*)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
American black bear (*Ursus americanus*)	Pads, fruits	Hoffmeister (1986); McClinton et al. (1992); Hellgren (1993)
Ringtail (*Bassariscus astutus*)	Fruits	Leopold (1959); Hoffmeister (1986)

(*continued on next page*)

TABLE 7.1 *(continued)*

	Mammals (continued)	
Species	Part(s) consumed	Reference
Raccoon (*Procyon lotor*)	Fruits	Dalquest (1953); Gonzalez-Espinoza and Quintana-Ascencio (1986); Lehman (1984)
White-nosed coati (*Nasua narica*)	Fruits	Hoffmeister (1986)
North American badger (*Taxidea taxus*)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Hooded skunk (*Mephitis macroura*)	Fruits	"
Mammoth (*Mammuthus* sp.)	Fruits	Davis et al. (1984)
Feral burro (*Equus asinus*)	Stems, pads	Krausman et al. (1989); Hicks andMauchamp (1995)
Wild boar (*Sus scrofa*)	Pads	Baber and Coblentz (1987)
Collared peccary (*Pecari tajacu*)	Pads, petals, fruits	Dalquest (1953); Eddy (1961); Zervanos and Hadley (1973); Everitt et al. (1981); Bissonette (1982); Sowls (1984); Corn and Warren (1985); Gonzalez-Espinoza and Quintana-Ascencio (1986); Hoffmeister (1986); Janzen (1986); Luévano et al. (1991); Martinez-Romero and Mandujano (1995)
Camel (*Camelus dromedarius*)	Pads	Janzen (1986)
Mule deer (*Odocoileus hemionus*)	Pads, fruits	Krausman (1978); Janzen (1986); Krausman et al. (1989)
White-tailed deer (*O. virginianus*)	Pads, fruits	Quinton and Horejst (1977); Arnold and Drawe (1979); Everitt and Gonzalez (1979); Quinton et al. (1979); Everitt et al. (1981); Gonzalez-Espinoza and Quintana-Ascencio (1986); Hoffmeister (1986); Luévano et al. (1991)
Pronghorn (*Antilocapra americana*)	Pads, fruits	Russell (1964); Stelfox and Vriend (1977); Sexson et al. (1981); Janzen (1986)
American bison (*Bison bison*)	Fruits	Janzen (1986)
Bighorn sheep (*Ovis canadensis*)	Pads, fruits	Hoffmeister (1986); Dodd and Brady (1988); Krausman et al. (1989)
Steenbok (*Raphicerus campestris*)	Pads	Marais (1939)
Feral goat (*Capra hircus*)	Stems, pads	Eliasson (1968); Thorton (1971); Hicks and Mauchamp (1995)

Consumption of Vegetative Structures

Four of the nine reptiles that forage on nopales consume their cladodes (pads). These include two tortoises and two land iguanas (scientific names also in Table 7.1). Only 16% of bird species consume the pads, but at least 43% of mammal species, including the Pleistocene Shasta ground sloth and mammoth, do, or did, so. Consumption of vegetative structures is mostly restricted to the pads for mammals, and exclusively so for reptiles (Table 7.2). Only black-tailed jackrabbits, Botta's pocket gopher, and feral burros and goats consume trunks and/or roots. *Opuntia* pads are a staple for only a few species (packrats, rabbits and jackrabbits, javelina, Galápagos tortoise, Galápagos land iguanas, and occasionally deer), although in some cases they only become a staple under drought conditions. Many of the consumers eat platyopuntias only sporadically.

Cladode Preferences

Most studies reporting nopales in herbivore diets derive their data from fecal analysis, which does not allow for knowledge about differences in preference for different cladodes of the plant. However, a difference in the palatability of young versus old cladodes would be expected. Indeed, Berlandier's tortoise prefers the younger, more tender cladodes that have fewer spines (Rose and Judd 1982). In contrast, rabbits and black-tailed jackrabbits consume the outer cladodes of *Opuntia violacea* var. *macrocentra*

TABLE 7.2
Percentage of animals within each major taxon that consume different parts of platyopuntias

Taxon	Number	Percent						
		Roots	*Trunks*	*Pads*	*Petals*	*Pollen and nectar*	*Fruits*	*Seeds*
Reptiles	9	0	0	44	67	22	67	0
Birds	26	0	0	19	4	35	69	38
Mammals	54	2	7	42	4	2	61	15
Overall	89	1	4	36	10	13	64	20

first, and then progress to the inside of the plants. This process is more as a result of the architectural arrangement of the plant, rather than due to differences in palatability of the cladodes (Hoffman et al. 1993).

When different platyopuntia species are available in the habitat, herbivores apparently prefer some over others. In a test with three platyopuntia species and one cholla species typical of *nopaleras* (nopal communities) in the San Luis Potosí–Zacatecas Plateau, Mexico, white-throated packrats prefer *Opuntia robusta* and *O. streptacantha* over *O. leucotricha* and *O. imbricata* (Rangel and Mellink 1993). *Opuntia robusta* and *O. streptacantha* have the lowest amounts of protein and highest amounts of fiber (Flores Valdez and Aguirre Rivera 1989), so the higher consumption by these packrats is not a response to nutritional quality. Rather, it apparently results from these cacti having fewer spines and glochids, which facilitates their consumption. Collared peccaries prefer one of two different morphs of the same subspecies of *O. phaeacantha,* again favoring the one with fewer spines (Theimer and Bateman 1992). However, in New Mexico, spinescence apparently does not affect grazing intensity by lagomorphs; rather, plant size and grazing history appear to be the factors that most determine grazing intensity; the proportion of grazed pads increases for plants that have more than seven cladodes (Hoffman et al. 1993).

Nopal growers and researchers indicate that some varieties of cultivated platyopuntias are more prone to consumption by wildlife than are others. So, 'Copena F1,' a spineless forage nopal, is preferred by rodents and lagomorphs over other spineless varieties in central Mexico (C. A. Flores-Valdés and F. Torres, personal communication). In some cases, lagomorphs can entirely wipe out a commercial orchard of this variety. However, spines are not a requirement for effective mechanical defense. Near Jacumba, California, black-tailed jackrabbits will eat almost anything except *Opuntia basilaris* (A. M. Rea, personal communication). This species does not have large spines; rather, it is densely covered with fine glochids (small, easily detached spines), a nasty encounter for herbivores.

To determine if white-throated packrats had foraging preferences among different cultivated varieties of *Opuntia ficus-indica,* rows of cultivars 'Roja,' 'Amarilla,' and 'Blanca' were examined at Las Papas de Arriba, Jalisco, Mexico. Packrats clearly prefer to consume cladodes of 'Roja' over 'Amarilla' and prefer 'Amarilla' over 'Blanca' (Table 7.3). Packrats build their dens on the ground against and around the trunks of platyopuntias using various materials (e.g., cladodes, twigs, dung, garbage). As there are no differences in the percentage of plants associated with packrat dens among different varieties (Table 7.3), differences in consumption must be attributed to the forage quality of the plants. The higher sugar content of 'Roja' presents one logical explanation for packrats' preference.

Seasonal Effects for Herbivory

In xeric habitats where free water is scarce, cladodes become an important source of water, when they are available. Not unexpectedly, vertebrates increase their use of *Opuntia* cladodes during the dry season, or use them only then. For example, rabbits and black-tailed jackrabbits consume *Opuntia* cladodes during the dry season, or when annuals are scarce and other perennials have not developed new growth (Hoffman et al. 1993). Berlandier's tortoises consume more cladodes during the summer, as a source of water (Auffenberg and Weaver 1969). Galápagos land iguanas reduce their preference for cladodes from about 32% of bites in the dry season to 5% after the rains (Christian et al. 1984). Even finches, doves, and mockingbirds drink fluids and eat moist pulp from cladodes in the Galápagos Islands (Grant and Grant 1981). Other animals consume platyopuntias under special conditions; e.g., pronghorn antelope feed readily on cladodes after a wildfire has burned off the spines (Stelfox and Vriend 1977).

TABLE 7.3

Differences in feeding by packrats and evidence from packrat dens for adjacent rows of different varieties of *Opuntia ficus-indica* cultivated in Las Papas de Arriba, Jalisco, Mexico

	Nopal variety		
Parameter	*'Roja'*	*'Amarilla'*	*Statistical significance*
Platyopuntias with evidence of feeding by packrats (% of plants)	45	19	< 0.0001
Platyopuntias associated with packrat dens (% of plants)	8	12	n.s.
	'Amarilla'	*'Blanca'*	*Statistical significance*
Platyopuntias with evidence of feeding by packrats (% of plants)	20	4	< 0.01
Platyopuntias associated with packrat dens (% of plants)	6	16	n.s.

Unpublished observations of E. Mellink and M. E. Riojas-López.

The white-throated packrat is one of the vertebrates that relies most heavily on platyopuntias for its food (Vorhies and Taylor 1940; Spencer and Spencer 1941; Rangel and Mellink 1993). Although *Opuntia* cladodes are its preferred food, seasonal variations in preference occur. In Arizona, this species exhibits clear peaks in consumption of cladodes in May and November (Vorhies and Taylor 1940), which coincides with the driest period of the year.

The vertebrate most popularized as a cladode eater is the collared peccary. Such fame is not undue, as platyopuntias are one of its most important food resources in arid lands. Indeed, *Opuntia* cladodes are the most common food for the peccary throughout the southwestern United States and northern Mexico (Neal 1959; Leopold 1959; Sowls 1984; Hoffmeister 1986). Peccaries are not ruminants, but their ruminant-like digestion allows them to use profitably such a high-fiber forage (Langer 1979). Despite their year-round high consumption of platyopuntias, collared peccaries exhibit seasonal variation, consuming them in greater quantities during the summer (Corn and Warren 1985) or fall (Eddy 1961). In northern San Luis Potosi, Mexico, collared peccaries steadily increase the amount of cladodes in their diet from 25% in June to 66% in September (Luévano et al. 1991). Cladode consumption during the summer may be associated with high temperatures, and peccaries as well as white-tailed deer presumably require the water for thermoregulation (Zervanos and Hadley 1973). During drought, a collared peccary must consume at least 2,300 g of succulent plants per day to thermoregulate effectively (Langer 1979).

Deer are not always regarded as consumers of cladodes, but in some arid regions they can rely heavily upon them, at least during certain times of the year. In Big Bend National Park, Texas, *Opuntia engelmannii* makes up 14% of the yearly diet of mule deer and 10% of that of white-tailed deer (Krausman 1978). At other localities in Texas, *Opuntia* cladodes form 30 to over 50% of the white-tailed deer's diet (Everitt and Gonzalez 1979; Quinton and Horejsi 1977). Deer consume the cladodes both for energy and as a source of water for thermoregulation (Arnold and Drawe 1979). Maximum cladode consumption by deer has been reported to occur in the spring (Krausman 1978), summer (Arnold and Drawe 1979), and summer/fall (Quinton and Horejsi 1977). Even within a given season, great month-to-month variation occurs in the amount of *Opuntia* cladodes consumed by deer (Luévano et al. 1991). Differences in the timing of peak consumption reflect water needs by the deer, along with the availability of free water and other succulents that might provide water. Less-studied animals also change their dependence on cladodes during the year, depending on other available resources. For example, the northern pocket gopher consumes cladodes the entire year, but in dramatically higher percentages during the winter, when the land is covered by snow and little other food is available (Vaughan 1967).

Nutritional Qualities of Cladodes

Platyopuntia cladodes make a rather poor forage. Their protein content varies between 3 and 13% (on a dry weight basis), depending on the species, time of the year, whether

the plant bears fruit, the particular cladode, and the age of the plant (Sowls 1984; Retamal et al. 1987; Flores Valdez and Aguirre Rivera 1989; Pimienta-Barrios 1990; Gregory and Felker 1992; Theimer and Bateman 1992). Moreover, while some platyopuntias exhibit variations in protein and phosphorus content associated with cladode age, others do not (Gregory and Felker 1992). Still, at even the highest level, the protein content is generally not sufficient for a substantive diet. For example, when collared peccaries are fed exclusively a cladode diet, they lose weight, but when protein is supplemented, not only do they maintain their weight, but some even gain weight (Sowls 1984). Collared peccaries also demonstrated vitamin B deficiencies when fed only cladodes (Sowls 1984). Regardless of its low nutritional value, the water provided by the cladodes is often critical for the survival of consumers and appears to be more important than any nutritional shortcomings at various times of the year. In any case, vertebrates seldom feed only on platyopuntias, and the inclusion in their diet of other plants with more protein, or invertebrates, prevent them from severe undernutrition.

Not only are *Opuntia* cladodes a less than optimal food for vertebrates, but there are also other risks associated with their consumption. When collared peccaries are forced to consume large quantities of nopales, large amounts of water flow through the digestive system, causing an almost continuous diarrhea (Sowls 1984), which can have serious consequences in arid lands. Probably the best known negative consequence of feeding on platyopuntias comes from the high levels of the oxalates in them (Hodgkinson 1977; Sowls 1984; Gibson and Nobel 1986). Dietary oxalates bind calcium (Ca), magnesium (Mg), sodium (Na), and potassium (K) as highly insoluble compounds and, in sufficiently high doses, commonly leads to hypocalcemia (James 1972; Hodgkinson 1977; Sowls 1984; Gibson and Nobel 1986). The binding with Ca and Mg is likely the strongest (E. Ezcurra, personal communication). Ill effects of high oxalic acid intake by mammals include nephritis and respiratory failure (Hodgkinson 1977; Sowls 1984). Although calcium oxalate crystals may cause mechanical damage to the digestive system (James 1972), those of *Opuntia* cladodes are rather rounded, as opposed, for example, to crystals in agaves, and may not be sufficiently abrasive to be a major problem (E. Ezcurra, personal communication).

However, herbivores that have intestinal or ruminal microflora capable of digesting cellulose can also degrade calcium oxalate and absorb the calcium, if given enough time for their digestive microbiota to adapt (Allison and Cook 1981; Justice 1985). This appears to be the case with packrats and other rodents (Shirley and Schmidt-Nielsen 1967; Justice 1985). This ability is provided by the adaptability of the digestive microflora itself, and does not represent an evolutionary adaptation of the herbivores (Justice 1985). Herbivores cope with dietary oxalates in at least one other way. Collared peccaries select inner cladodes that have lower levels of oxalates (although lower spininess seems to be also involved in this selection), but because these cladodes also have less protein and more lignin, the peccaries sacrifice diet quality (Theimer and Bateman 1992). Nopales also contain high quantities of alkaloids (Meyer et al. 1980; Gibson and Nobel 1986). These substances could harm consumers of platyopuntias, but not enough is known about them and their potential effects on herbivores.

Spine Effects on Herbivory

Spines can potentially inflict wounds that can become infected (Anthony 1954). Several vertebrates, e.g., the collared peccary (Theimer and Bateman 1992) and white-throated packrats (Rangel and Mellink 1993), feed less on the more spiny cladodes. In the Galápagos Islands, spines effectively prevent young arborescent platyopuntias from being consumed by tortoises (Biggs 1990). However, Berlandier's tortoises feeding on cladodes are not hindered much by spines, as several individuals with large spines in the masseter muscles on both sides of the neck have been observed (Auffenberg and Weaver 1969).

In addition to selecting cladodes that are less spiny, vertebrates often scrape the spines off. For example, collared peccaries sometimes bite through the entire cladode, but most commonly they step on it, peel the skin (epidermis plus hypodermis) off one side, and then eat the pulp (Sowls 1984). Captive Galápagos land iguanas fed cladodes often scrape the surface with a front foot to remove the spines before biting into the pad (Carpenter 1969). In platyopuntia orchards in Jalisco, desert cottontails discard the areoles and spines along with little pieces of cuticle when feeding on cladodes. This explains the abundant pieces of cuticle found at the bases of platyopuntias, together with cottontail rabbit fecal pellets. Platyopuntias that have only jackrabbit pellets and no cuticle pieces suggest that the jackrabbits handle the spines in a different manner. White-throated packrats, in addition to selecting less spiny plants, most often gnaw across the cladode, beginning somewhere along its edge, and then work their way inward, possibly discarding the spines and glochids along the way (Fig. 7.1A). At other times they feed by scraping the pulp from the side of the cladode (Fig. 7.1B). In spite of the hazards that might be involved, the animals that rely on *Opuntia* cladodes for an important part of

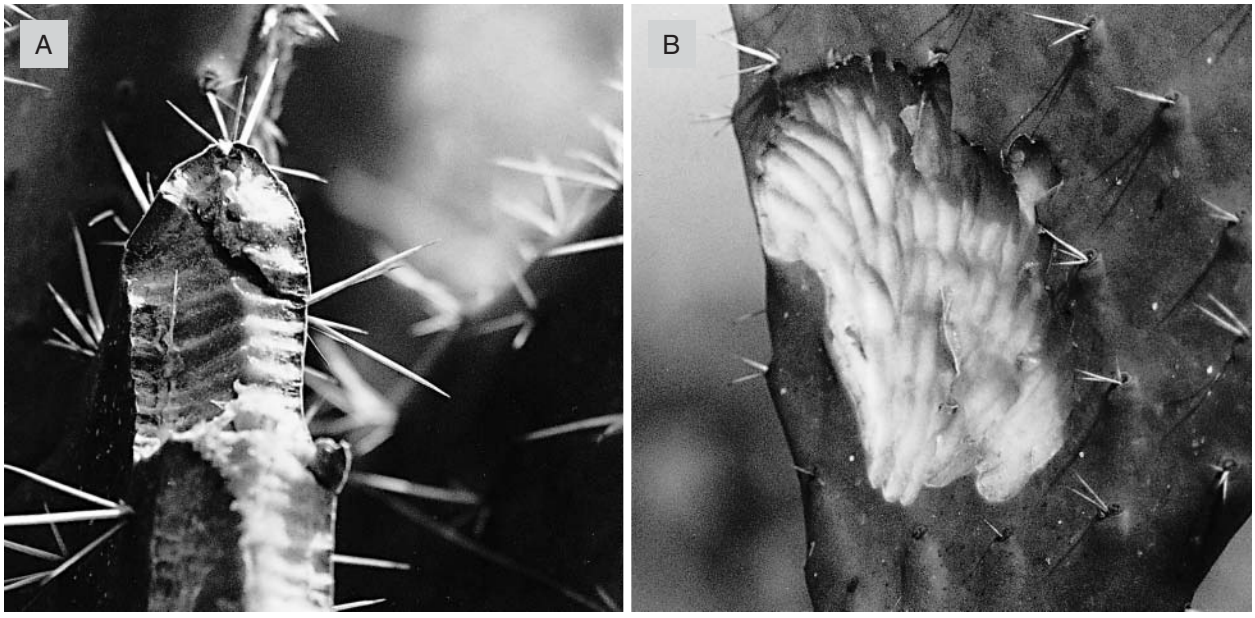


Figure 7.1. Cladodes exhibiting signs of feeding by packrats near Las Papas, Jalisco, Mexico: (A) feeding on the edge and (B) feeding on the side.

their diet are able to cope with this resource, and death induced by such consumption in free-ranging conditions is rather uncommon.

Consumption of Reproductive Structures

The reproductive structures of platyopuntias, especially fruits and seeds, are the major source of attraction to consumers. All the reptilian and bird consumers eat them, as do most of the mammalian consumers (Table 7.1). Actually, given a chance, all mammals that consume vegetative platyopuntia structures may readily eat flowers and fruits as well. Flowers and fruit are available seasonally, but the seeds can be available all year, because fruits ripen asynchronously, and because seeds can remain on the ground for long periods.

Consumers of reproductive structures are of three foraging types: (1) primary foragers—those that directly reach the flowers or fruits to feed on them; (2) secondary consumers—those that that feed on flowers or fruits once they have been made available by a previous consumer; and (3) tertiary consumers that feed on seeds, including those of platyopuntias that are in the feces of other consumers, e.g., kangaroo rats, pocket mice, and canyon towhees, among others (Gonzalez-Espinoza and Quintana-Ascencio 1986). A primary consumer may open a fruit, allowing a secondary consumer to reach its interior, or it may cause petals, fruits, or seeds to fall to the ground. Once a fruit has been pried open by a primary consumer, such as a packrat, a host of other users might eventually feed on it. These secondary consumers will include not only insects—ants, bugs, wasps (Fig. 7.2)—but also birds and rodents (Gonzalez-Espinoza and Quintana-Ascencio 1986).

Flower Consumption

Flowers provide more energy for herbivores than do the cladodes or the fruits but only modest amounts of protein (Christian et al. 1984). So the nutritive quality does not seem to explain the "enthusiasm with which the iguanas scramble for a newly fallen flower, nor does it demonstrate the willingness of the iguanas to travel from tree to tree to consume fallen flowers of *Opuntia*" (Christian et al. 1984). Indeed, two-thirds of the reptiles that consume platyopuntias specifically eat the flowers (Table 7.2). Pollen and nectar contained in the flowers might be part of the explanation for such a preference.

Some bird species on the Galápagos Islands consume pollen and nectar during the dry season, switching to fruits, seeds, and arthropods during the rainy season (Grant and Grant 1979, 1981; Millington and Grant 1983). During the dry season when other foods are scarce, the cactus finch on Daphne Major relies almost exclusively on pollen and nectar, which seem to provide sufficient nutrients for pre-rain breeding. This is an advantage because pairs of this finch that start breeding before the rains produce more offspring (Grant 1996). This finch is a true cactus specialist. To some extent, it excludes the other finches from feeding on pollen and nectar of platyopuntias, defending larger territories year-round, which is in contrast



Figure 7.2. Nopal fruit used as food source by a wasp after a primary consumer has pried it open, near Las Papas, Jalisco, Mexico.

with other finches on Daphne Major, who defend smaller territories and only for part of the year (Grant and Grant 1981; Grant 1996). Indeed, the ground finch on Daphne Major consumes much lower amounts of nopal pollen and nectar, and the onset of its breeding season is after the rains (Grant 1996).

Doves on the Galápagos Islands feed on *Opuntia* flowers, possibly first removing the stamens and nectar, and then tearing and eating the petals. This seems to be a rather unusual feeding habit—not often observed and not exhibited by all dove populations (Grant and Grant 1979). Lava lizards on Pinta Island climb up platyopuntias and tear the petals to obtain the pollen. In contrast, the lava lizard on Daphne Major does not climb platyopuntias but obtains pollen opportunistically by eating the pollen-impregnated petals that fall when the Daphne Major cactus finch feeds (East 1995). The lizards probably obtain an important portion of protein from the pollen, especially as the onset of *Opuntia* flowering occurs during the dry season when arthropods are in short supply (East 1995). Even the Lagarto Tizón, an omnivorous lizard of the Canary Islands, Spain, feeds on platyopuntia pollen (Valido and Nogales 1994).

Pollen has variable levels of protein. Notably, pollen from bat-pollinated cactus flowers has a high protein content, e.g., up to 44% in the saguaro, but pollen of the non-bat-pollinated *Opuntia versicolor* has only 9% protein (Howell 1974). In addition to their protein content, pollen grains are valuable because they contain essential amino acids and vitamins (Howell 1974; Grant and Grant 1981; Millington and Grant 1983; Richardson et al. 1986; Grant 1996). Galápagos finches digest over 90% of the pollen they consume (Grant 1996). The physiology of such high digestibility has not been clarified, but either the Galápagos finches and lava lizards (which also exhibit a high digestion of pollen) are especially efficient, or platyopuntia pollen is quite easy to digest (Grant 1996). Several paths are theoretically possible in the digestion of pollen; for a small, pollen-eating marsupial (*Tarsipes rostratus*), pollen seems to be digested directly through the pores in its exine coat (Richardson et al. 1986). Consuming nectar along with pollen, in addition to providing energy, may also help the ingested pollen germinate, facilitating its digestion (Grant 1996).

Fruit Consumption

Opuntia fruits are a valuable food resource for animals and are readily eaten when available. Over 60% of platyopuntia consumers in any taxa eat the fruits. Platyopuntia fruits (tunas) have 9 to 18% sugar and large quantities of vitamin C (Pimienta-Barrios 1990). Fruits of *Opuntia lindheimeri* from southern Texas have 7% protein, 0.15% phosphorus (P), 2.5% Ca, 0.93% Mg, 3.4% K, and 0.02% Na (Everitt and Alaniz 1981). Vertebrates may consume fruits as a "gourmet" food, when they encounter them, as the Shasta ground sloth did (Hansen 1978). On the Canary Islands, the endemic Lagarto Tizón consumes fruits of *Opuntia dillenii* during May (Valido and Nogales 1994). As different platyopuntia species bear fruits of different sizes, color, and spininess, foraging preferences of vertebrates differ (Janzen 1986).

The seeds are used by at least 13 vertebrate herbivores, mostly birds (Table 7.2). They are also an important resource for many rodents (González-Espinoza and Quintana-Ascencio 1986). Such seeds are rich in oils and proteins (Pimienta-Barrios 1990). Although seeds may be available year-round, certain vertebrates eat them only when other resources are in short supply. In the Galápagos Islands during the dry season, seed consumption by the Daphne Major cactus finch declines as flower feeding increases (Millington and Grant 1983).

Evolutionary and Ecological Context

Past and Present Herbivory Pressures

In arid and semiarid lands, platyopunitas often constitute one of the most conspicuous elements of the landscape, and it is easy to find relationships among them and some

vertebrates. Platyopuntias provide protein, carbohydrates, and water to vertebrates, and these vertebrates in turn act as pollinators and dispersers (Grant and Grant 1979; Gonzalez-Espinoza and Quintana-Ascencio 1986; Biggs 1990; East 1995). However, these relationships do not explain the evolution of the traits currently exhibited by platyopuntias and their fruits. Rather, platyopuntias on continental America are the ghosts of past interactions that involve currently extinct megaherbivores (Janzen and Martin 1982; Gonzalez-Espinoza and Quintana-Ascencio 1986; Janzen 1986). On the Galápagos Islands, the evolutionary pressures, which are still operational, are different.

According to Janzen (1986), not only did Pleistocene megaherbivores shape the form and anatomy of platyopuntias, but they also could have dispersed them from South to North America, or vice versa, after the closure of the Central American bridge. In addition to being long-distance dispersers in Pleistocene communities, some megaherbivores probably munched their way through dense patches of platyopuntias, creating clearings that would be colonized by other plants and, perhaps, small mammals, reptiles, and invertebrates. After most of the megaherbivores of the Americas vanished at the end of the Pleistocene, platyopuntias have maintained most of the traits developed under the pressure of their former consumers. Certainly, important changes in distribution and abundance resulted from the absence of their principal dispersers, but the species survived. In a few cases, erosion of anachronistic traits (*sensu* Janzen and Martin 1982) seems to be occurring; e.g., some platyopuntia species have "spiny" fruits that are not eaten by herbivores and which are mostly sterile (Anthony 1954).

Although they might have contributed little to the past shaping of platyopuntias, the extant opuntiofagous vertebrates do currently serve as dispersers of seeds. Birds remove only modest amounts of seeds—less than 5% of the total crop (Janzen 1986)—but rodents can remove more seeds from the fruits once they fall to the ground (Gonzalez-Espinoza and Quintana-Ascencio 1986). Rodent caches often become the source of new platyopuntias away from the mother plants. The seed shadows produced by extant vertebrate dispersers are surely much different—and at smaller geographical scales than from those that can be presumed for Pleistocene megaherbivores (Janzen 1986). Nonetheless, these extant vertebrates may substantially increase the cover of platyopuntia communties, especially when patterns of competition among different plants is altered by the introduction of alien grazers, such as cattle or sheep (Riegel 1941; Timmons 1942). The effects of direct removal of platyopuntia parts by extant species on the system are difficult to assess. For example, collared peccaries can remove 2 to 5% of the cladodes (Bissonette 1982). As platyopuntias are well armored against grazing, direct removal of large parts of their vegetative structure is unlikely (and probably was unlikely even during the Pleistocene), except during severe drought.

Galápagos Islands

Nowhere is the association between platyopuntias and vertebrates as intense as on the Galápagos Islands. The morphology of nopales on different islands is a clear adjustment to avoid herbivory on vegetative structures (Thornton 1971; Biggs 1990; Hicks and Mauchamp 1995). Arborescent platyopuntias predominate on specific islands of the Galápagos that support, or have supported, tortoise and land iguana populations. These plants have large scaly trunks (> 60 cm in height), bearing rounded compact crowns with lower cladodes strongly armored with spines and the upper cladodes almost spineless. When young, spines protect these nopales from grazing by tortoises. On islands that have never supported tortoises or iguanas, the plants are decumbent and have weak or no spines, some cladodes bearing only tufts of glochids (Biggs 1990). During the rainy season, some cladodes of arborescent platyopuntias become heavy, turgid with water, and break off from the mother plants, falling to the ground. There they maintain a high water content, even through the following dry season, when they are the main food source for land iguanas and tortoises (Biggs 1990).

A particularly strong relationship exists between birds and platyopuntias in the Galápagos Islands. In its simplest form, differences in size and hardness of platyopuntia seeds may be a partial response to predation by finches. Conversely, the size and shape of the beaks of finches may reflect an adjustment to forage efficiently for pollen and nectar, as well as the ability to break seeds (Grant and Grant 1989). Some finches contribute significantly to the cross-pollination of platyopuntias, transporting pollen from plant to plant. Such transport is important, as flowers that receive pollen from flowers of the same plant produce significantly fewer seeds than those that receive pollen from more distant plants (Grant and Grant 1981). Consequently, these finches promote larger seed crops.

However, this pollinating service is not without negative repercussions. When feeding on flowers, the finches often snip off the styles, presumably to facilitate access to the pollen, which prevents fertilization of the ovules. As a result, by obtaining energy and protein from nectar and pollen, the finches benefit by having an early onset of their



Figure 7.3. Feral burro eating the fruit of *Opuntia* aff. *megacantha* near Las Papas, Jalisco, Mexico.

breeding season, but, in doing so, threaten the seed supply for their dry-season feeding (Grant and Grant 1981). The negative effect of snipping styles might be only partial: the later the style is snipped, the greater the chance that the pollen has already reached the stigma and some ovules are fertilized (Grant and Grant 1981). Despite their overall value as pollinators, finches sometimes cause damage to platyopuntia trunks and young cladodes when pecking into them to drink fluid, eat storage tissues, and take insect larvae (Grant and Grant 1981). As a result, the damaged pads are vulnerable to infection by bacteria and fungi, eventually leading to necrosis.

The preceeding is a highly simplified picture of the relationships that have shaped the Galapágos Islands platyopuntias and their communities. The real picture is more complex and involves variations at different time scales. Regrettably, the conditions that promoted the evolution of the local relationships have not remained intact. The land reptiles have been hunted, sometimes to extinction, and alien species have been introduced (Thornton 1971; Hicks and Mauchamp 1995). These events have already affected the permanence of such relationships and probably will cause others that might be detrimental to the conservation of the entire platyopuntia-associated system.

Alienized Relations

Whenever platyopuntias have been introduced to other parts of the world, they have been readily accepted by local vertebrates. Ten animals have been reported to consume introduced platyopuntias (Leopard tortoise, Lagarto Tizón, ostrich, emu, black magpie, little raven, baboon, "monkeys," camel, and steenbok; Table 7.1), but there are probably many more unreported consumers. Frequently, native vertebrates may become dispersers of alien platyopuntias, which is the case for the Lagarto Tizón (Valido and Nogales 1994) on the Canary Islands, the black magpie in Australia (Darnell-Smith 1919), and primates and birds in South Africa (Weed Section 1940). Other native vertebrates that consume alien platyopuntia fruits may also disperse seeds. Alien vertebrates may also disperse alien platyopuntias, as demostrated by feral European rabbits in Australia (Darnell-Smith 1919). The roster of opuntiofagous vertebrates in areas were platyopuntias are alien is surely much larger than what has been reported so far (Table 7.1), and it is unlikely that it will ever be fully reported.

The other side of the coin in alienized relations is that of the impact of alien vertebrates on native platyopuntias. Four alien species currently consume cladodes in the wild in the Americas (black rat; feral burro, Fig. 7.3; wild boar;

and feral goat). When cattle and horses roamed wild two centuries ago, they likely also engaged in cladode consumption, as domestic individuals of these species do today. In continental America, the introduction of large domestic vertebrates (namely, cattle and horses) restored functions interrupted by the extinction of megafauna at the end of the Pleistocene (Martin 1975; Janzen 1986), although this view is not always accepted. In insular contexts, however, the introduction of alien herbivores or omnivores often causes conservation hazards, if not mass extinction, even for well-protected species, such as platyopuntias.

Three alien vertebrates threaten platyopuntias on the Galápagos Islands. Goats feed on the pads of nopal (Hicks and Mauchamp 1995). They munch through the trunks of arboreal platyopuntias, up to 50 cm in diameter, causing them to fall (Eliasson 1968). Medium and large platyopuntias are subject to a higher grazing pressure, because they are less spiny, and this selection can seriously impair platyopuntia populations, as it leads to the killing of the plants before they reach reproductive age (Hicks and Mauchamp 1995). Fallen cladodes can produce new trees, but the goats eagerly eat the pads before any rooting takes place (Hicks and Mauchamp 1995). Burros have also affected the distribution of platyopuntias on the Galápagos Islands (Van der Werff 1982; Hicks and Mauchamp 1995). In the case of seedlings, their heavy spiny armour can prevent grazing by native reptiles but does not prevent goats from considering them a "favorite" (Schofield 1989). While not evident at first consideration, mice (probably *Mus musculus*) are also a threat to platyopuntias on the Galápagos Islands (Snell et al. 1994). They burrow among and into the roots, weakening their hold on the soil. The effect of such activities and the success of prevention programs in the long run is difficult to predict.

Concluding Remarks

Platyopuntia cladodes offer not only food and water, but also protective cover, den anchorage, and den building materials to wild vertebrates. Several species are closely associated with platyopuntias: Berlandier's tortoise, white-throated packrat, collared peccary, and deer, as well as finches, land iguanas, and tortoises on the Galápagos Islands. Other vertebrates rely on cladodes for survival during critical periods such as drought. Still other species, although not using the cladodes themselves, use the native platyopuntia nopaleras as habitat.

Despite the fact that several relationships between platyopuntias and vertebrates exist, there has been a paucity in the efforts to understand them, except for the highly creative studies on the Galápagos Islands. For the continental Americas, the advances in understanding platyopuntia-vertebrate interactions notably include the proposal of Janzen (1986) on the evolution of platyopuntias, their communities, and their dispersal in North America as well as the work of González-Espinoza and Quintana-Ascencio (1986) on *Opuntia* seed dispersal for nopaleras in the Mexican plateau. Most other work has focused on the role of cladodes in the diet of selected vertebrates, especially the collared peccary. Clearly, much research remains to be done to understand the function of nopaleras in the continental Americas. If such an understanding is to be generated, action should be taken soon, as nopaleras are being modified at accelerated rates to raise agricultural products or livestock, or as an inevitable side effect of human population growth.

Acknowledgments

We thank Rosy Licón, Roberto García-Benitez, Dolores Sarracino, and Park Nobel, who helped obtain some of the bibliographic sources, and Amadeo Rea and Exequiel Ezcurra for insightful reviews.

Literature Cited

Allison, M. J., and H. M. Cook. 1981. Oxalate degradation by microbes of large bowel of herbivores: The effect of dietary oxalate. *Science* 212: 675–676.

Anthony, M. 1954. Ecology of the Opuntiae in the Big Bend region of Texas. *Ecology* 35: 334–347.

Arnold, L. A., Jr., and D. L. Drawe. 1979. Seasonal food habits of white-tailed deer in the south Texas plains. *Journal of Range Management* 32: 175–176.

Auffenberg, W., and W. G. Weaver. 1969. *Gopherus berlandieri* in southern Texas. *Bulletin of the Florida State Museum* 13: 141–203.

Baber, D. W., and B. E. Coblentz. 1987. Diet, nutrition, and conception in feral pigs on Santa Catalina Island. *Journal of Wildlife Management* 51: 306–317.

Bailey, V. 1931. Mammals of New Mexico. *North American Fauna* 53: 1–412.

Biggs, A. L. 1990. Coevolution in the Galápagos. *American Biology Teacher* 52: 24–28.

Bissonette, J. A. 1982. Ecology and social behavior of the collared peccary in Big Bend National Park. *National Park Service Scientific Monograph* 16: 1–85.

Blair, W. F. 1937. The burrows and food of the prairie pocket mouse. *Journal of Mammalogy* 18: 188–191.

Bowman, R. I. 1961. Morphological differentiation and

adaptation in the Galápagos finches. *University of California Publications in Zoology* 58: 1–302.

Brown, D. E. 1989. *Arizona Game Birds.* University of Arizona Press, Tucson.

Burt-Davy, J. 1920. Utilizing prickly pear and spineless cactus. *South African Journal of Industry* 3: 1001–1011.

Carpenter, C. C. 1969. Behavioral and ecological notes on the Galápagos land iguanas. *Herpetologica* 25: 155–164.

Christian, K. A., C. R. Tracy, and W. P. Porter. 1984. Diet, digestion, and food preferences of Galápagos land iguanas. *Herpetologica* 40: 205–212.

Clements, F. E., and V. E. Shelford. 1939. *Bio-Ecology.* Wiley, New York.

Corn, J. L., and R. J. Warren. 1985. Seasonal habits of the collared peccary in south Texas. *Journal of Mammalogy* 66: 155–159.

Dalquest, W. W. 1953. Mammals of the Mexican state of San Luis Potosí. *Lousiana State University Studies, Biological Sciences Series* 1: 1–112.

Darnell-Smith, G. P. 1919. Animal aids to the spread of prickly pear. *Agricultural Gazette of New South Wales* 30: 125–127.

Davis, O. K., L. Agenboard, P. S. Martin, and J. I. Mead. 1984. The Pleistocene blanket of Bechan Cave, Utah. *Special Publication of Carnegie Museum of Natural History* 8: 267–282.

Dodd, N. L., and W. W. Brady. 1988. Dietary relationships of sympatric desert bighorn sheep and cattle. *Desert Bighorn Council Transactions* 1988: 1–6.

Dunn, J. P., J. A. Chapman, and R. E. Marsh. 1982. Jackrabbits. In *Wild Mammals of North America* (J. A. Chapman and G. A. Feldhamer, eds.). Johns Hopkins University Press, Baltimore, Maryland. Pp. 124–145.

East, K. T. 1995. Pollen digestion in Galápagos lava lizards. *Noticias de Galápagos* 55: 8–14.

Eddy, T. A. 1961. Foods and feeding patterns of the collared peccary in southern Arizona. *Journal of Wildlife Management* 25: 248–257.

Eliasson, U. 1968. On the influence of introduced animals on the natural vegetation of the Galápagos Islands. *Noticias de Galápagos* 11: 19–21.

Everitt, J. H., and M. A. Alaniz. 1981. Nutrient content of cactus and woody plant fruits eaten by birds and mammals in south Texas. *Southwestern Naturalist* 26: 301–305.

Everitt, J. H., and C. L. Gonzalez. 1979. Botanical composition and nutrient content of fall and early winter diets of white-tailed deer in south Texas. *Southwestern Naturalist* 24: 297–310.

Everitt, J. H., C. L. Gonzalez, M. A. Alaniz, and G. V. Latigo. 1981. Food habits of the collared peccary on south Texas rangelands. *Journal of Range Management* 34: 141–144.

Flores Valdez, C. A., and J. R. Aguirre Rivera. 1989. *El Nopal como Forraje,* 2nd ed. Universidad Autónoma Chapingo, Chapingo, Mexico.

Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer.* Harvard University Press, Cambridge, Massachusetts.

Gonzalez-Espinoza, M., and P. F. Quintana-Ascencio. 1986. Seed predation and dispersal in a dominant desert plant: Opuntia, ants, birds, and mammals. In *Frugivores and Seed Dispersal* (A. Estrada and T. H. Fleming, eds.). W. Junk, Dordrecht, The Netherlands. Pp. 273–284.

Grant, B. R. 1996. Pollen digestion by Darwin's finches and its importance for early breeding. *Ecology* 77: 489–499.

Grant, B. R., and P. R. Grant. 1981. Exploitation of *Opuntia* cactus by birds on the Galápagos. *Oecologia* 49: 179–187.

Grant, B. R., and P. R. Grant. 1989. Natural selection in a population of Darwin's finches. *American Naturalist* 133: 377–393.

Grant, P. R., and K. T. Grant. 1979. Breeding and feeding ecology of the Galápagos dove. *Condor* 81: 397–403.

Gregory, R. A., and P. Felker. 1992. Crude protein and phosphorus contents of eight contrasting *Opuntia* clones. *Journal of Arid Environments* 22: 323–331.

Hansen, R. M. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. *Paleobiology* 4: 302–319.

Hellgren, E. C. 1993. Status, distribution, and summer food habits of black bears in Big Bend National Park. *Southwestern Naturalist* 38: 77–80.

Hicks, D. J., and A. Mauchamp. 1995. Size-dependent predation by feral mammals on Galápagos *Opuntia. Noticias de Galápagos* 55: 6–17.

Hodgkinson, A. 1977. *Oxalic Acid in Biology and Medicine.* Academic Press, New York.

Hoffman, M. T., J. D. James, G. I. H. Kerley, and W. G. Whitford. 1993. Rabbit herbivory and its effects on cladode, flower and fruit production of *Opuntia violacea* var. *macrocentra* (Cactaceae) in the northern Chi-

huahuan Desert, New Mexico. *Southwestern Naturalist* 38: 309–315.

Hoffmeister, D. F. 1986. *Mammals of Arizona.* University of Arizona Press, Tucson.

Howell, D. J. 1974. Bats and pollen: Physiological aspects of syndrome of chiropterophyly. *Comparative Biochemistry and Physiology, Series A* 48: 263–276.

James, L. F. 1972. Oxalate toxicosis. *Clinical Toxicology* 5: 231–243.

Janzen, D. H. 1986. Chihuahuan Desert nopaleras: Defaunated big mammal vegetation. *Annual Review of Ecology and Systematics* 17: 595–636.

Janzen, D. H., and P. S. Martin. 1982. Neotropical anachronisms: The fruits the gomphotheres ate. *Science* 215: 19–27.

Justice, K. E. 1985. Oxalate digestibility in *Neotoma albigula* and *Neotoma mexicana. Oecologia* 67: 231–234.

Krausman, P. R. 1978. Forage relationships between two deer species in Big Bend National Park, Texas. *Journal of Wildlife Management* 42: 101–107.

Krausman, P. R., B. D. Leopold, R. F. Seegmiller, and S. G. Torres. 1989. Relationship between desert bighorn sheep and habitat in western Arizona. *Wildlife Monographs* 102: 1–66.

Lack, D. 1947. *Darwin's Finches.* Cambridge University Press, Cambridge, England.

Langer, P. 1979. Adaptational significance of the fore stomach of the collared peccary, *Dicotyles tajacu* (L. 1758) (Mammalia: Artiodactyla). *Mammalia* 43: 235–245.

Lehman, V. W. 1984. *Bobwhites in the Rio Grande Plains of Texas.* Texas A&M University Press, College Station, Texas.

Leopold, A. S. 1959. *Wildlife of Mexico.* University of California Press, Berkeley.

Long, A., R. M. Hansen, and P. S. Martin. 1974. Extinction of the shasta ground sloth. *Geological Society of America Bulletin* 85: 1843–1848.

Luévano E. J., E. Mellink, E. García M., and R. Aguirre R. 1991. Dieta y traslapo dietario del venado cola blanca, jabalí de collar, cabra y caballo, durante el verano en la Sierra de la Mojonera, Vanegas, S.L.P. *Agrociencia, serie Recursos Naturales Renovables* 1: 105–122.

MacCracken, J. G., and R. M. Hansen. 1984. Seasonal foods of blacktail jackrabbits and Nuttall cottontails in southeastern Idaho. *Journal of Range Management* 37: 256–259.

Marais, J. G. 1939. Spineless cactus and old-man saltbush for sheep. *Farming in South Africa* 1939: 99–100.

Martin, P. S. 1975. Vanishings, and future, of the prairie. *Geoscience and Man* 10: 39–49.

Martinez-Romero, L. E., and S. Mandujano. 1995. Habitats alimentarios del pecarí de collar (*Pecari tajacu*) en un bosque tropical caducifolio de Jalisco, Mexico. *Acta Zoologica Mexicana* 64: 1–20.

McClinton, S. F., P. L. McClinton, and J. V. Richerson. 1992. Food habits of black bears in Big Bend National Park. *Southwestern Naturalist* 37: 433–435.

McCulloch, E. M. 1980. Little raven *Corvus mellori* eating fruit of prickly pear *Opuntia* sp. *Australian Bird Watcher* 8: 248.

McLure, M. F., N. S. Smith, and W. W. Shaw. 1995. Diets of coyotes near the boundary of Saguaro National Monument and Tucson, Arizona. *Southwestern Naturalist* 40: 101–105.

Meyer, B. N., A. H. Mohamed, and J. L. MacLaughlin. 1980. β-phenethylamines from the cactus genus *Opuntia. Phytochemistry* 19: 719–720.

Mijares-Urrutia, A., B. Colvée, and A. Arend R. 1997. Sauria: *Cnemidophorus lemniscatus* (NCN). Herbivory. *Herpetological Review* 28: 88.

Millington, S. J., and P. R. Grant. 1983. Feeding ecology and territoriality of the cactus finch *Geospiza scandens* on Isla Daphne major, Galapagos. *Oecologia* 58: 76–83.

Milton, S. J. 1992. Plants eaten and dispersed by adult leopard tortoises *Geochelone pardalis* (Reptilia: Chelonii) in the southern Karoo. *South African Journal of Zoology* 27: 45–49.

Neal, B. J. 1959. A contribution on the life history of the collared peccary in Arizona. *American Midland Naturalist* 61: 177–190.

Pimienta-Barrios, E. 1990. *El Nopal Tunero.* Universidad de Guadalajara, Zapopan, Mexico.

Price, T. 1987. Diet variation in a population of Darwin's finches. *Ecology* 68: 1015–1028.

Quinton, D. A., and R. G. Horejsi. 1977. Diets of white-tailed deer on the rolling plains of Texas. *Southwestern Naturalist* 22: 505–509.

Quinton, D. A., R. G. Horejsi, and J. T. Flinders. 1979. Influence of brush control on white-tailed deer diets in north-central Texas. *Journal of Range Management* 32: 93–97.

Rangel, M. G., and E. Mellink. 1993. Historia natural de la rata magueyera en el Altiplano Mexicano. In *Avances*

en el Estudio de los Mamíferos de México (R. A. Medellín and G. Ceballos, eds.). Asociación Mexicana de Mastozoología, Mexico City. Pp. 173–183.

Retamal, N., J. M. Duran, and J. Fernandez. 1987. Seasonal variation of chemical composition in prickly pear (*Opuntia ficus-indica* [L.] Miller). *Journal of the Science of Food and Agriculture* 38: 303–311.

Richardson, K. C., R. D. Wooler, and B. G. Collins. 1986. Adaptations to a diet of nectar and pollen in the marsupial *Tarsipes rostratus* (Marsupialia: Tarsipedidae). *Journal of Zoology* 208: 285–297.

Riegel, A. 1941. Some coactions of rabbits and rodents with cactus. *Transactions of the Kansas Academy of Sciences* 44: 96–101.

Rose, F. L., and F. W. Judd. 1982. Biology and status of Berlandier's tortoise (G*opherus berlandieri*). In *North American Tortoises: Conservation and Ecology* (R. B. Bury, ed.). Wildlife Resarch Report 12. United States Fish and Wildlife Service, Washington, D.C. Pp. 57–70.

Russell, P. T. 1964. *Antelope of New Mexico.* New Mexico Department of Fish and Game, Santa Fe.

Schluter, D. 1984. Body size, prey size and herbivory in the Galápagos lava lizard, *Tropidurus. Oikos* 43: 291–300.

Schofield, E. K. 1989. Effects of introduced plants and animals on island vegetation: Examples from the Galápagos Archipelago. *Conservation Biology* 3: 227–238.

Sexson, M. L., J. R. Choate, and R. A. Nicholson. 1981. Diet of pronghorn in western Kansas. *Journal of Range Management* 34: 489–493.

Shirley, E. K., and K. Schmidt-Nielsen. 1967. Oxalate metabolism in the pack rat, sand rat, hamster, and white rat. *Journal of Nutrition* 91: 496–502.

Snell, H. L., H. M. Snell, and P. Stone. 1994. Accelerated mortality of *Opuntia* on Isla Plaza Sur: Another threat from an introduced vertebrate? *Noticias de Galápagos* 53: 19–21.

Sowls, L. K. 1984. *The Peccaries.* University of Arizona Press, Tucson.

Spaulding, W. G., and P. S. Martin. 1979. Ground sloth dung of the Guadalupe mountains. *National Park Service Proceedings* 4:259.269.

Spencer, D. A., and A. L. Spencer. 1941. Food habits of the white-throated wood rat in Arizona. *Journal of Mammalogy* 22: 280–284.

Stelfox, J. G., and H. G. Vriend. 1977. Prairie fires and pronghorn use of cactus. *Canadian Field Naturalist* 91: 282–285.

Theimer, T. C., and G. C. Bateman. 1992. Patterns of prickly-pear herbivory by collared peccaries. *Journal of Wildlife Management* 56: 234–240.

Thornton, I. 1971. *Darwin's Islands; a Natural History of the Galápagos.* American Museum of Natural History, Garden City, New York.

Timmons, F. L. 1942. The dissemination of prickly pear seed by jack rabbits. *Journal of the American Society of Agronomy* 34: 513–520.

Valido, A., and M. Nogales. 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70: 403–411.

Van der Werff, H. 1982. Effects of feral pigs and donkeys on the distribution of selected food plants. *Noticias de Galápagos* 36: 17–18.

Vaughan, T. A. 1967. Food habits of the northern pocket gopher on shortgrass prairie. *American Midland Naturalist* 77: 176–189.

Vorhies, C. T., and W. P. Taylor. 1922. Life history of the kangaroo rat *Dipodomys spectabilis spectabilis* Merriam. *Bulletin of the United States Department of Agriculture* 1091: 1–40.

Vorhies, C. T., and W. P. Taylor. 1933. The life histories and ecology of jack rabbits, *Lepus alleni* and *Lepus californicus* ssp., in relation to grazing in Arizona. *University of Arizona College of Agriculture Technical Bulletin* 49: 471–587.

Vorhies, C. T., and W. P. Taylor. 1940. Life history and ecology of the white-throated wood rat, *Neotoma albigula albigula* Hartley, in relation to grazing in Arizona. *University of Arizona College of Agriculture Technical Bulletin* 86: 455–529.

Weed Section [South African] Department of Agriculture and Forestry. 1940. Opuntias in South Africa. I: Some naturalized species with special reference to prickly pear, and methods for its eradication. *Farming in South Africa* 15: 119–125.

Zervanos, S. M., and N. F. Hadley. 1973. Adaptational biology and energy relationships of the collared peccary (*Tayassu tajacu*). *Ecology* 54: 759–774.

CHAPTER

› 8 ‹

BIODIVERSITY AND CONSERVATION

Thomas H. Boyle and Edward F. Anderson

Introduction
Biodiversity of Cacti
Biodiversity of Natural Communities of Cacti
Genetic Diversity in Wild Cacti
Breeding Systems and Sexual Expression in the Cactaceae
Biodiversity of Cultivated Cacti
Conservation of Cacti
Why Cacti Are Threatened
Determination of Threatened Cacti
Conservation of Specific Cacti
Importance of Artificial Propagation
CITES
The Convention on Biological Diversity
In situ *and* ex situ *Conservation*
Conclusions and Future Prospects
Literature Cited

Introduction

Cacti have been exploited since pre-Columbian times. Many cacti have fruits that are eaten raw, cooked, or fermented into alcoholic beverages. Stems of some cacti are cooked as a vegetable, used as an emergency source of water, or fed to domestic animals as forage or fodder. Dried woody stems of some large columnar cacti are gathered for building material or firewood. Some species produce substances of pharmaceutical or industrial interest (e.g., cochineal dye extracted from the dried bodies of a scale insect [*Dactylopius coccus*] collected from many species of prickly-pear cacti), whereas other cacti are consumed to induce visual hallucinations for religious or recreational purposes. Last but not least, cacti are prized for their diverse forms and beautiful flowers and are cultivated worldwide as ornamentals. Unfortunately, habitat destruction and collection of wild cacti has threatened the very survival of some species, and attention now must be focused on their protection.

The conservation of biodiversity is one of the major issues facing humankind today and is of paramount importance for the long-term survival of cacti as well as other organisms. This chapter examines the biodiversity of both wild and cultivated cacti, and discusses contemporary and long-term issues pertaining to conservation of cacti. Factors affecting biodiversity of cacti and the estimation of genetic diversity in wild and cultivated cacti are considered

first. Then the effects of habitat destruction and collection on biodiversity loss of wild cacti are discussed and international activities that encourage the conservation of cacti are presented.

Biodiversity of Cacti

The term *biodiversity* refers to the range of variation or differences exhibited by biological organisms and their environments (Barbier 1997). Biodiversity is essential for the adaptation to specific environments and for the continuing evolution of species. It may refer to variation present within a gene, an organism, a species (with extinction representing the total and irreversible loss of biological diversity), a population, or an ecosystem (or community). Scientists, conservationists, and policymakers are interested in several aspects of biodiversity, including the maintenance of biodiversity, the impact of biodiversity loss, and the establishment of priorities for biodiversity conservation. However, a single biodiversity indicator does not apply to all conservation issues. Reid et al. (1993) listed 22 indicators relating to different conservation issues and grouped them into three categories: (1) those used for estimating diversity within wild species; (2) those used for estimating diversity in domesticated plants and animals, e.g., crops or livestock; and (3) those used for estimating diversity within communities or habitats. For this review, biodiversity of cacti will be examined in each of these three conservation systems.

Biodiversity of Natural Communities of Cacti

Cacti inhabit a wide diversity of climatic regions and ecosystems throughout much of the New World. Their range extends from 58°N latitude in Canada (*Opuntia fragilis*) to 50°S in Patagonia (*Maihuenia, Opuntia, Pterocactus*); in South America, from the islands of Fernando de Noronha off Brazil's Atlantic coast to the Galápagos Archipelago in the Pacific; and, in North America, from the coast of Massachusetts (*Opuntia humifusa*) to southern Vancouver Island (*O. fragilis;* Barthlott and Hunt 1993). Their altitudinal distribution varies from coastal habitats throughout much of North and South America to about 4,500 m in the Andean uplands of Peru and Chile (*Austrocylindropuntia floccosa, A. lagopus;* formerly *Opuntia floccosa* and *O. lagopus;* Barthlott and Hunt 1993). Cacti are most plentiful in the arid and semiarid regions between 35°N and 35°S (Taylor 1997), but about 10% of all species are epiphytic or epilithic and are found in more humid regions (Barthlott 1983). Species of cacti are sparse toward the periphery of the family's range and in its equatorial center but relatively abundant in four geographical regions, or centers of diversity (Table 8.1). Collectively, these four centers of diversity contain approximately half of all known species of cacti and substantial numbers of endemics. Two other regions, i.e., the Caribbean basin (including northern Venezuela, Panama, and northern and western Colombia) and Chile (excluding the northeastern corner [see Table 8.1]), also contain numerous endemics.

TABLE 8.1
Centers of diversity and endemism for the Cactaceae

Geographic region	Endemic genera	Species present
Mexico; southwestern United States	28	570
Central Andes of Peru and Bolivia, southern Ecuador, northeastern Chile, northwestern Argentina	19	535
Eastern Brazil	12	145
Central western and southern Brazil, Paraguay, Uruguay, southern and eastern Argentina	—	85

Data are from Taylor (1997) for the approximately 125 genera in the Cactaceae and for species on the CITES Cactaceae checklist (Hunt 1992).

A primary objective of conservation is to maintain species diversity within a defined locale or region. In most cases, species diversity has been interpreted as "species richness," i.e., the quantity of species within a country, ecosystem, or region. For cacti, as for other species, species diversity is greatest in the centers of diversity; e.g., one locale in northeast Mexico has 27 species of cacti (Taylor 1997). An emphasis on preserving plant communities with the greatest species richness has meant that the major focus of conservation measures in the Americas has been on tropical moist broadleaf forests ("rainforests") rather than the drier, nonforested or semiforested regions (Redford et al. 1990). However, this latter group of ecosystems contains the vast majority of cacti. Hence, many of the conservation measures designed to preserve tropical rainforests in the Americas have had little impact on conservation of cacti.

Genetic Diversity in Wild Cacti

Wild species of plants experience numerous changes in their biological and physical environment over time. Their survival, evolutionary potential, and ability to adapt to environmental changes will depend on the existence of genetic diversity. As a consequence, considerable effort has been made to estimate the genetic diversity within wild species of plants. Information on genetic diversity in wild

species has come primarily from allozyme surveys. Allozymes exhibit simple inheritance, codominance, complete penetrance, and consistency of expression under a wide range of environmental conditions and can be determined for a wide range of plant species irrespective of natural habitat, size, or longevity (Hamrick 1989). These properties make allozymes particularly useful as genetic markers.

Allozyme surveys estimate the level of genetic diversity within individual species and indicate how the genetic variation is distributed within and among populations. A typical allozyme survey consists of three parts: (1) collection of allozyme data from a minimum of one population (usually more) of a species, (2) computation of diversity statistics, and (3) comparison of the species' diversity statistics with those collected from other species with similar life history traits (Hamrick and Godt 1989, 1996). The following statistics are calculated at the species and within-population levels: (1) percentage of polymorphic loci (*P*), (2) mean number of alleles per locus (*A*) for polymorphic as well as monomorphic loci, and (3) genetic diversity (*H*) of each locus ($H = 1 - \sum p_i^2$, where p_i is the mean frequency of the *i*th allele at a locus). Mean genetic diversity at the species and within-population levels is determined by averaging the *H* values over all loci. For the average plant species, *P, A,* and *H* values are 50%, 1.96, and 15%, respectively (Hamrick and Godt 1989). The *P, A,* and *H* values for the average plant population are 34%, 1.53, and 11%, respectively. For studies that examine allozyme variation in multiple populations, the genetic diversity within populations (H_S) and the total genetic diversity (H_T) are computed for polymorphic loci, and the G_{ST} statistic is calculated to estimate the proportion of total diversity among populations ($G_{ST} = [H_T - H_S]/H_T$ [Nei 1973]). For the average plant species, about 78% of the total genetic diversity (H_T) at polymorphic loci resides within populations, whereas 22% of the H_T is distributed among populations (Hamrick and Godt 1989).

Allozyme surveys have been conducted on natural populations of *Opuntia humifusa* (Wallace and Fairbrothers 1986), *Pachycereus schottii* (Parker and Hamrick 1992), and *Weberbauerocereus weberbaueri* (Sahley 1996). The most thorough genetic diversity study on wild cacti was on the diploid ($2n = 22$) species *P. schottii* (formerly *Lophocereus schottii;* Parker and Hamrick 1992). Eight populations of *P. schottii* were examined at the northern extremity of its range (southern Arizona), where reproduction is primarily asexual. At the species level, the percent polymorphic loci was 44%, the mean number of alleles per locus was 1.55, and the mean genetic diversity (H_e) was 0.145. The *P* value for *P. schottii* (44%) was comparable to the mean *P* value reported by Hamrick and Godt (1989) for dicots (45%), species with a narrow distribution range (45%), and species that reproduce sexually and asexually (44%). The mean proportion of polymorphic loci and mean genetic diversity (H_e) within populations were 34% and 0.126. The mean proportion of total diversity among populations (G_{ST}) was 0.13. Thus, about 87% of the total genetic variation occurred within populations. The mean G_{ST} value for *P. schottii* was lower than for groups of species with similar ecological traits—dicots, species with a narrow distribution range, species that disperse seed by animal ingestion, and species that reproduce sexually and asexually (Hamrick and Godt 1989). Sporadic long-distance dispersal of stems and occasional sexual reproduction apparently helped sustain a level of genetic diversity in *P. schottii* that is similar to sexually reproducing species. Previous studies (Ellstrand and Roose 1987; Hamrick and Godt 1989) have shown that species that reproduce primarily or exclusively by asexual means (vegetative reproduction and/or agamospermy) maintain as much genetic diversity as species that reproduce sexually.

Information about the extent and distribution of genetic variation in plant species has both scientific merit and practical applications. For example, allozyme data can be useful for determining how to collect and maintain genetically representative samples for conserving genetic diversity in *ex situ* collections. Information on the distribution of genetic variation within and among populations has aided in the development of sampling strategies for collecting plant materials of endangered species (Brown and Briggs 1991).

Breeding Systems and Sexual Expression in the Cactaceae

The breeding system markedly affects the magnitude and distribution of genetic diversity in plant species. The Cactaceae can be roughly divided into two groups, depending on whether they are predominantly outcrossing or primarily selfing. Most cacti probably outcross to some degree, and many species are likely to be predominantly outcrossing. Cacti exhibit several mechanisms that encourage outcrossing, including self-incompatibility, herkogamy, and dicliny. Self-incompatibility is a genetically controlled mechanism that promotes outcrossing in fertile hermaphrodites by preventing fertilization when a plant is selfed or outcrossed to another plant with the same incompatibility phenotype (de Nettancourt 1977). It is widespread in the Cactaceae and has been documented in at least 30 of its approximately 120 genera (Boyle 1997). These genera comprise all three of the traditional Cactaceae subfamilies

(Pereskioideae, Opuntioideae, and Cactoideae) and eight of the nine Cactoideae tribes. Self-incompatibility can minimize inbreeding, but, as pointed out by Olmstead (1986), the extent of inbreeding within a population depends primarily on population size rather than on the type of breeding system. Genetic diversity is rapidly lost from small populations due to inbreeding and genetic drift (random changes in allelic frequencies; Wilcox 1984).

Dicliny occurs when some members of a population normally produce flowers that are unisexual instead of hermaphroditic and has been reported in several Cactaceae taxa. Dioecy (co-occurrence of androecious and gynoecious plants) occurs in *Echinocereus coccineus* (Hoffmann 1992) and *Opuntia stenopetala* (Parfitt 1985). Gynodioecy (consisting of hermaphroditic and gynoecious plants) has been reported in *Mammillaria dioica* (Ganders and Kennedy 1978; Parfitt 1985) and *M. neopalmeri* (Parfitt 1985). Trioecy (co-occurrence of androecious, gynoecious, and hermaphroditic plants) occurs in *P. pringlei* (Fleming et al. 1994) and *Selenicereus innesii* (Innes and Glass 1991). Hermaphroditic, dioecious, and trioecious populations have been documented for *Opuntia robusta* (Parfitt 1985; del Castillo 1986; Hoffmann 1992). Each type of dicliny promotes outcrossing but to different degrees. Dioecy ensures 100% outcrossing. With gynodioecy and trioecy, the level of outcrossing depends on the frequency of females in the population, degree of selfing in hermaphrodites, and pollinator activity. Murawski et al. (1994) used allozyme analysis to examine the mating system in *P. pringlei* (a self-compatible trioecious species); the estimated proportion of outcrossing in females was nearly 1.0 (0.949) but the proportion was markedly lower (0.30) in hermaphroditic individuals, indicating that the majority of seeds produced by hermaphrodites result from selfing.

Pollen must be transferred between plants with dissimilar incompatibility phenotypes or dissimilar floral morphologies (diclinous taxa) for seed to set. As far as is known, cacti are pollinated exclusively by animals (Porsch 1938, 1939; Rowley 1980; Grant and Grant 1979; Grant and Hurd 1979; Schlindwein and Wittmann 1997). Animals also serve as dispersal agents for fruit and seed of cacti (Gates 1932; Wallace and Fairbrothers 1986). Hence, cacti and their animal pollinators/dispersers have developed mutualistic relationships, with animals receiving nectar and/or pollen as a reward for pollination or, in the case of seed/fruit dispersal, receiving nutrients from the fruit pulp or digested seeds. The incapacity to set seed due to absence of pollinators has profound effects on the genetic structure, mating system, and selection forces of obligately outcrossed species (Olesen and Jain 1994). Any disturbance to mutualistic plant-animal relationships may affect the survival and continuing evolution of either partner. Two night-blooming columnar cacti (*P. pringlei* and *Stenocereus thurberi*) in Sonora, Mexico, may be falling below their reproductive potential possibly due to the scarcity of *Leptonycteris* bats (Fleming et al. 1996). The population sizes of three columnar cacti (*Cereus repandus, Pilosocereus lanuginosus,* and *Stenocereus griseus*) growing on Curaçao, Netherlands Antilles, are decreasing due to unregulated land development threatening the survival of two species of nectar-feeding bats (*Leptonycteris curasoae curasoae* and *Glossophaga longirostris elongata;* Petit and Pors 1996). Conservation efforts should focus not only on endangered or threatened cacti but also on those animal species that are essential for their pollination and seed dispersal.

Biodiversity of Cultivated Cacti

Most of the information available on biodiversity of cultivated cacti comes from allozyme studies of two economically important ornamental cacti: Christmas cactus (*Schlumbergera*) and Easter cactus (*Hatiora;* formerly *Rhipsalidopsis*). The levels of genetic diversity in these two cacti (Table 8.2) are similar to those found in the "average" domesticated crop.

Chessa et al. (1997) used allozymes to analyze an Italian collection of 33 prickly pear (*Opuntia ficus-indica*) clones. Seven enzyme systems were examined using cladode tissue and 10 enzyme systems using pollen. Allozyme polymorphism was detected for 2 enzyme systems with cladodes and 5 enzyme systems with pollen (29% and 50% polymorphism, respectively). Malate dehydrogenase was the most effective enzyme for distinguishing clones within the collection. Uzun (1997) examined allozymes in 15 Turkish ecotypes and 3 Italian cultivars of prickly pear using 7 enzyme systems. All cultivars displayed the same banding patterns, suggesting that genetic diversity among *O. ficus-indica* ecotypes and cultivars is low. Neither of these allozyme studies provided genetic interpretations of isozyme banding patterns for *O. ficus-indica,* which is required for calculating genetic diversity statistics.

Genetic diversity in cultivated cacti is limited by the restricted number of progenitors and the loss of genetic variation in cultivation. Most of the domesticated cacti grown for fruit or ornamental flowers apparently originated from a relatively narrow germplasm base. In the case of Easter cactus, over 100 distinct clones have been described (Meier 1995), but all probably are descendants of three plants (two *Hatiora gaertneri* and one *H. rosea*) collected in the field in the late 19th and early 20th centuries. Loss of genetic variation commonly occurs during crop domestication due to

TABLE 8.2
Genetic diversity for clonal germplasm collections of Christmas cactus (*Schlumbergera*) and Easter cactus (*Hatiora*)

Plant	Number of clones analyzed	Polymorphic loci (%)	Mean number of alleles per locus	Mean heterozygosity
Christmas cactus	44	75	2.17	0.24
Easter cactus	40	54	1.85	0.21
Crops	—	49	2.15	0.19

Calculations are based on 12 loci for Christmas cactus and 13 loci for Easter cactus (O'Leary and Boyle 1999, 2000) or 18 crop plants (Doebley 1989).

culling undesirable plants, random loss of alleles, and changes in gene frequencies because of adaptation to the *ex situ* environment. O'Leary and Boyle (1999) found that a collection of 40 Easter cactus clones (which included field-collected clones, older cultivars, and modern cultivars) exhibit greater genetic diversity than a subset of 13 modern cultivars that make up the bulk commercial production. Isozyme profiles indicate that many of the uncommon alleles found in older Easter cactus cultivars are not present in modern cultivars. Thus, the reduced level of genetic diversity in modern cultivars results from loss of alleles during breeding and selection.

Other factors tend to preserve the level of genetic diversity in cultivated cacti. Unlike crops like corn or wheat that have been cultivated for millennia, most cultivated cacti have been domesticated relatively recently and thus have not been subject to intensive breeding and selection. For example, field-collected plants of *Schlumbergera truncata* and *H. gaertneri* were not introduced into cultivation until 1818 and 1882, respectively. Also, most of the economically important cacti are propagated asexually (except for breeding new cultivars), which tends to conserve more of the initial genetic diversity compared to sexual propagation. Moreover, interspecific hybridization is widely practiced with ornamental cacti and tends to increase the level of genetic diversity, as for Easter cactus. Most cultivated clones of Easter cactus are complex interspecific hybrids of *H. gaertneri* and *H. rosea* (= *H.* × *graeseri* [Werderm.] Barthlott). Although flower color is quite limited in two progenitor species (*H. gaertneri* has scarlet-red flowers whereas *H. rosea* has rose-pink flowers), the flower color range in *H.* × *graeseri* includes shades of red, lavender, purple, and pink to salmon and golden-orange (Meier 1995).

Although overcollection is a significant problem that threatens the survival of some wild cacti, the opposite problem occurs for many cultivated cacti, i.e., low genetic diversity due to insufficient collection from wild sources. Barthlott et al. (2000) reported that all 58 of the species in tribe Rhipsalideae are in cultivation, but eight of these species (*Lepisium micranthum, L. miyagawae, Rhipsalis ewaldiana, R. hoelleri, R. juengeri, R. pentaptera, Schlumbergera kautskyi,* and *S. orssichiana*) are likely to be represented by a single clone. *Rhipsalis pentaptera,* for example, is cultivated in more than 100 botanic gardens (Barthlott et al. 2000), but there is no genetic diversity among cultivated specimens because they are all derived from vegetative propagation of a single plant. The geophyte *Echinopsis chamaecereus* (formerly *Chamaecereus silvestrii;* Fig. 8.1) represents another case of restricted biodiversity in cultivated cacti. It is one of the most popular ornamental cacti and is grown for its unique finger-like shoots and bright scarlet flowers. However, all of the *E. chamaecereus* plants in cultivation apparently originated from one self-incompatible clone (R. Kiesling, personal communication). Low genetic diversity in cultivated cacti restricts the development of new cultivars by conventional plant breeding techniques.

The importance of conserving cultivars of economically useful cacti is often overlooked but needs to be addressed (Given 1994). Cultivars often contain unique assemblages of genes that may be useful for future breeding efforts. Plant breeders rely primarily on cultivars as the genetic resource for developing new varieties (Frankel et al. 1995). Aside from their economic value, cactus cultivars can be useful for both applied and basic research because they often can be cultivated more readily than wild taxa.

Conservation of Cacti

Human activities are having a heavy impact on populations of cacti, whether that impact is the destruction of natural habitats or overcollecting by hobbyists and commercial dealers. Careless collectors have left piles of dying cacti in the field (Fig. 8.2), and mining activities, road construction, and farming have destroyed prime habitat for

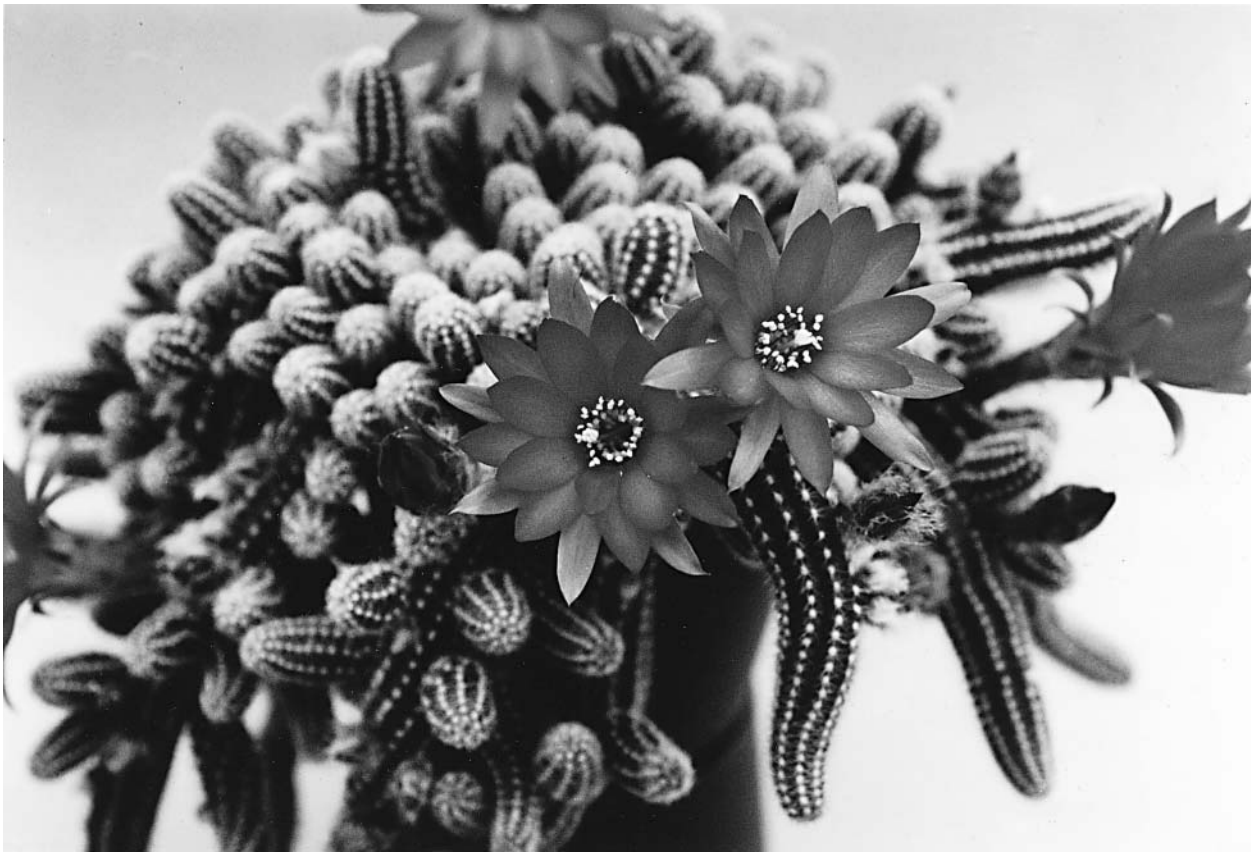


Figure 8.1. *Echinopsis chamaecereus* (formerly *Chamaecereus silvestrii*), commonly known as peanut cactus, is a popular ornamental species. The plants in cultivation apparently originated from vegetative propagation of a single, self-incompatible clone.

rare cacti. Indeed, cactus conservation faces a serious crisis. Unfortunately, there are few easy answers as to how cacti can be better protected because part of the problem rests with human nature.

Most people agree that conservation is a good thing. Unfortunately, many view conservation strictly in the abstract, not in the biological sense, where it properly lies. Also, there are disagreements among biologists themselves as to the best ways to conserve wildlife. Both plants and animals are part of the ecosystem; all have a function, though we may not easily recognize it. One can speak of the esthetic aspects of wildlife, or of the potential and actual contributions that plants and animals make to human existence, whether for food, fiber, beauty, medicine, or a myriad other things. Thus, most accept the fact that plants and animals should be protected, but some limit that protection to "whenever possible and appropriate." There are continuing struggles between conservationists and developers, between those that want to protect wildlife and those that wish to exploit it. Usually there are not easy answers or simple compromises between these differing parties. Hence, conservation efforts are frequently frustrated by well-intentioned groups that simply have different agendas. Education and communication are two critical tools that must be used if conservation efforts are to have a chance of success.

Some wish to lock up vast areas of land, restricting access to everyone so that natural populations of plants and animals will be permanently preserved. Others feel that living organisms should be an available resource for humans, and that natural events, such as extinction, should be allowed to proceed, especially when coming in conflict with human activities. Some believe that a few protected areas, botanic gardens, and zoos will be adequate for preserving at lease some of the natural diversity. Unfortunately, whatever conservation approach is used, extinction is irreversible, and the lost organism cannot be brought back again. Interestingly, few would disagree that one of the main functions of conservation is to perpetuate plants and animals so that future generations may benefit from them. The problem is how to best attain that goal. Conservationists often speak of the importance of plants as pos-

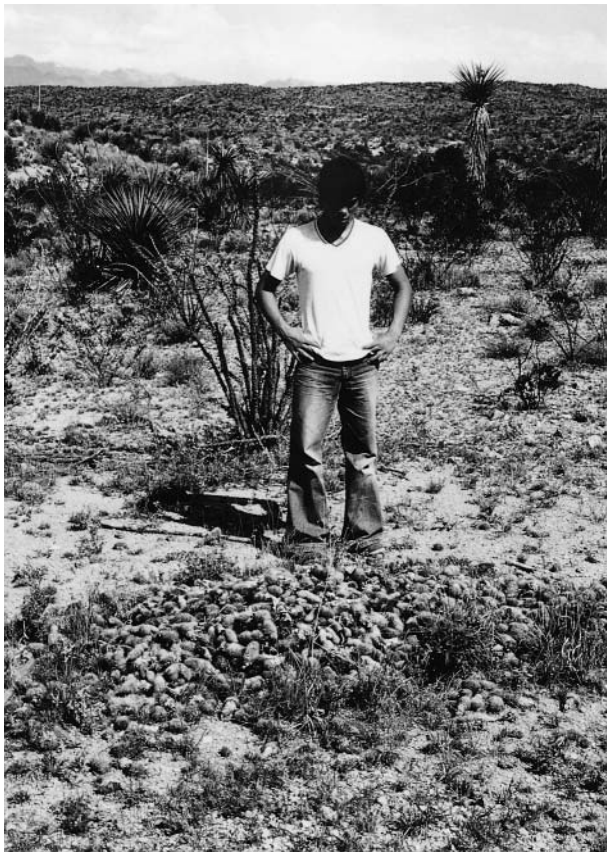


Figure 8.2. Pile of dead and dying cacti in the Big Bend Region of west Texas in 1982. Pictured is Duc Anderson, an assistant on a field study of rare cacti.

sible sources of drugs or other products of value to humans. Clearly, a strong case can be made for the conservation of plants, including cacti.

Why Cacti Are Threatened

Cacti, like many other plants, are seriously threatened by habitat destruction, whether for the development of new farmland, for expanding urban areas, or for other human activities, such as road building and mining. Many cacti are also threatened by collectors, who wish to either sell them in the trade or simply have them in personal collections. Cacti are remarkable organisms, and many people throughout the world enjoy collecting and propagating them. Unfortunately, a source of plants for trading or selling is needed, and this source often comes from wild populations. Millions of cacti are artificially propagated annually, thus satisfying many hobbyists (Fig. 8.3). However, some collectors are like "stamp collectors" in that they want as many "originals" as possible, meaning that the plants must come directly from the wild. Thus, uncommon and unusual cacti are frequently the victims of these unscrupulous collectors, who flout local and national laws to satisfy their personal needs. Conservationists agree that habitat destruction is one of the main factors that lead to extinction, but habitat destruction is only one of the causes of the disappearance of cacti, with illegal collecting being a significant cause.

These illegal activities have been frustrating to scientists. A goal of scientific research is to provide an accurate description of material being studied. However, scientists have quickly learned that unscrupulous collectors immediately visit sites, the descriptions of which have been published or recorded on herbarium sheets. In several instances most or all the plants have been removed, e.g. for *Aztekium ritteri.* A new locality for this species has been obtained so that it can be studied (Anderson and Skillman 1984); however, habitat information is presented only in broad generalities because of the threat of collectors, a dilemma faced by many researchers. In 1996 George Hinton described a new *Mammillaria* species, *M. luethii.* The few plants that have been seen and the photographs of this unusual cactus have caused a sensation among collectors, who wish to learn where it grows. Hinton and Jonas Lüthy, the discoverers of the plant, have not told anyone of its location because of its rarity and the near certainty that unscrupulous collectors would immediately devastate the wild population if the location were divulged. Rather, the two are arranging for the artificial propagation of the species to make it available to collectors. Again, however, proper science is thwarted by the need to protect the wild population.

Cactus researchers have long realized the importance of cactus conservation. In 1987 the Cactus and Succulent Specialist Group of the Species Survival Commission (SSC), an arm of the International Union for Conservation of Nature and Natural Resources (IUCN), was created. Scientists from many regions of the world collaborated in writing *Cactus and Succulent Plants: Status Survey and Conservation Action Plan* (Oldfield 1997). This document is the most comprehensive publication dealing with the conservation status of each succulent plant group, including cacti, as well as conservation measures and action proposals.

Determination of Threatened Cacti

The United States Endangered Species Act was passed in 1973 and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) came into existence in 1976. There was necessarily a rush to place plants that people thought were threatened or endangered on the lists. The first listing of cacti for CITES was creat-



Figure 8.3. Commercially grown cacti in California.

ed on 1 July 1975, and in several cases there were few data to support the decisions that were made. Indeed, the determination of what organism is threatened or endangered is difficult at best, but a strong effort has been made to create a useful system by which plants and animals are placed in various categories of threat. Nearly sixty species of cacti are currently listed in Appendix I of CITES (Table 8.3). Thirty species are listed as threatened or endangered in the United States (Table 8.4). This may seem like a small number when considering that there are about 1,700 species of cacti.

Studies of natural cactus populations since 1960 indicate two things: (1) not all seriously threatened cacti are on either of the lists; and (2) not all the plants on the lists may, in fact, be seriously threatened with extinction. The United States government asked scientists at the Desert Botanical Garden in Phoenix, Arizona, to monitor two species of cacti in the Big Bend region of Texas that were listed in the U.S. Endangered Species Act as Threatened: *Echinomastus* (= *Neolloydia* or *Sclerocactus*) *mariposensis* and *Coryphantha ramillosa* (Anderson and Schmalzel 1997; Schmalzel and Anderson 1999). Both species were found to be widespread and not seriously threatened with extinction. Scientists at the Desert Botanical Garden have also been involved in evaluating the conservation status of suspected rare cacti in Mexico, an effort sponsored by the World Wildlife Fund (Anderson et al. 1994). A joint team of Americans and Mexicans has been involved in a 3-year, CITES-sponsored cactus-monitoring project, also in Mexico (Anderson 1997). The two monitoring projects (in Mexico) provided much information about the conservation status of nearly 50 species of rare cacti.

Two new species of cacti, *Aztekium hintonii* and *Geohintonia mexicana,* were described in 1992 just prior to the beginning of the CITES-sponsored study, so they were initially included in the project because of the excitement produced among the cactus hobbyists and dealers and uncertainty about their conservation status. The discoverer of the plants, George Hinton, provided detailed information about the size and density of the populations of the two species, which grow sympatrically on gypsum rocks in Nuevo León. Both species are relatively widespread and

TABLE 8.3
Cacti listed in Appendix I of CITES (as of 1996), including endangered species for which international trade is banned

Ariocarpus (all 6 species)
Astrophytum asterias
Aztekium ritteri
Coryphantha werdermannii
Discocactus (all 5–6 species)
Echinocereus ferreirianus subsp. *lindsayi*
E. schmollii
Escobaria leei
E. minima
E. sneedii
Mammillaria pectinifera
M. solisioides
Melocactus conoideus
M. deinacanthus
M. glaucescens
M. paucispinus
Obregonia denegrii
Pachycereus militaris
Pediocactus bradyi
P. despainii
P. knowltonii
P. paradinei
P. peeblesianus
P. sileri (*Sclerocactus sileri*)
P. winkleri
Pelecyphora (both species)
Sclerocactus brevihamatus subsp. *tobuschii*
S. erectocentrus (*Echinomastus erectocentrus*)
S. glaucus
S. mariposensis (*Echinomastus mariposensis*)
S. mesa-verdae
S. papyracanthus
S. pubispinus
S. wrightiae
Strombocactus disciformis
Turbinicarpus (all 6 species)
Uebelmannia (all 2–4 species)

Updated taxonomy appears in parentheses.

numerous. However, extensive illegal collecting of plants occurred when a few individuals from eastern Europe learned where they grew, and some local villagers discovered that the plants could be sold and charged visitors for admission to the sites. Although the local villagers naturally resented efforts by conservationists to protect the populations and some illegal collectors were apprehended by Mexican authorities, the devastation of some sites continued. Artificially propagated material of both species is now available in the market, which has led to a reduction in the pressure on the wild populations. Ironically, the seeds and plants used as the source of this artificially propagated material were illegally removed from Mexico. This experience with *A. hintonii* and *G. mexicana* has created an interesting dilemma among hobbyists who have ethical concerns about the conservation of cacti. Artificially propagated plants may be purchased, but they are derived from illegally collected stock. However, these plants are also reducing the pressure to collect material from wild populations.

In 1980 the IUCN—The World Conservation Union (a nongovernmental organization created in Switzerland in 1948) established criteria and categories of threat for assessing extinction risks to species. An improved set of criteria and categories of threat was adopted in 1994, which were later used to assess some of the species that were listed in the 1996 IUCN Red List of Threatened Animals and the 1997 IUCN Red List of Threatened Plants. The latter publication lists 33,798 species as threatened, approximately one-eighth of the world's total vascular plants (Walter and Gillett 1998). The Red List has 581 cactus species, approximately 35% of the total number of species in the family. Probably this is a fairly accurate estimate of the conservation threat to the family.

Both category definitions and the criteria by which they are determined have been controversial, so a further revision of the categories is currently under way (IUCN/SSC Criteria Review Working Group 1999). A system that can be readily used on plant populations is needed, as the present IUCN categories of threat are difficult to apply unless extensive fieldwork is undertaken. The following are the proposed new categories of threat: (1) *Extinct*—no organisms exist; (2) *Extinct in the Wild*—organisms still exist but no longer in the wild; (3) *Critically Endangered*—facing an extremely high risk of extinction in the near future; (4) *Endangered*—not critically endangered but facing a very high risk of extinction in the wild in the near future; (5) *Vulnerable*—facing a high risk of extinction in the wild; (6) *Near Threatened*—do not qualify as threatened but may become so in the near future; (7) *Least Concern*—do not qualify for any of the above categories. The criteria are based on the evaluation of populations of organisms and a projection of their probable future, but data are often simply insufficient to classify the organism into one group or another. This is particularly true of the cacti, for few detailed, long-term studies have been carried out, underscoring one of the highest priorities for cactus conservation.

Conservation of Specific Cacti

Cacti have long been—and continue to be—used by Native Americans in both North and South America. Though their use as food sources has decreased with the improvement of transportation and Native Americans' par-

TABLE 8.4
Cacti listed as Endangered (E) or Threatened (T) in the U.S. Endangered Species Act (as of 1998), with updated taxonomy in parentheses

Taxon	Status
Ancistrocactus tobuschii (*Sclerocactus brevihamatus*)	E
Astrophytum asterias	E
Cereus eriophorus var. *fragrans* (*Harrisia fragrans*)	E
Coryphantha minima (*Escobaria minima*)	E
C. ramillosa	T
C. robbinsorum (*Escobaria robbinsorum*)	T
C. scheeri var. *robustispina* (*C. robustispina*)	E
C. sneedii var. *leei* (*Escobaria sneedii* subsp. *leei*)	E
C. sneedii var. *sneedii* (*Escobaria sneedii* subsp. *sneedii*)	E
Echinocactus horizonthalonius var. *nicholii*	E
Echinocereus chisoensis var. *chisoensis*	T
E. fendleri var. *kuenzleri*	E
E. lloydii (*E.* × *roetteri*)	E
E. reichenbachii var. *albertii* (*E. reichenbachii* subsp. *fitchii*)	E
E. triglochidiatus var. *arizonicus* (*E. coccineus*)	E
E. viridiflorus subsp. *davisii*	E
Echinomastus mariposensis	T
Harrisia portoricensis	T
Leptocereus grantianus	E
Opuntia treleasei (*O. basilaris* var. *treleasei*)	E
Pediocactus bradyi	E
P. despainii	E
P. knowltonii	E
P. peeblesianus var. *peeblesianus*	E
P. sileri (*Sclerocactus sileri*)	E
P. winkleri	T
Pilosocereus robinii (*P. polygonus*)	E
Sclerocactus glaucus	T
S. mesa-verdae	T
S. wrightiae	E

tial acculturation into Anglo and other societies, cacti still have importance for ceremonial and medicinal purposes. Central Mexico provides an example of local use of plants having a negative impact on wild populations. Two species of *Mammillaria, M. bocasana* and *M. plumosa,* are used locally for Christmas decorations, which has led to the complete destruction of some populations of these cacti near villages (W. A. Fitz Maurice, personal communication).

The peyote cactus (*Lophophora williamsii*) is a more serious example of the impending loss of a cactus in a specific region that is important in Native American culture. This plant is believed by many Native Americans to be a gift from God and a sacrament, and the tops of the plant are consumed as part of the religious ceremony of the Native American Church (Anderson 1995, 1996). The stems of this cactus contain the alkaloid mescaline, which affects the senses, often leading to enhanced visual experiences. Thousands of fresh or dried "buttons" (Fig. 8.4) are consumed annually in these all-night ceremonies involving singing, praying, and quiet contemplation. Hispanic "peyoteros," who are licensed by the state of Texas, harvest large quantities of the tops of the plants and sell them legally to Native Americans throughout the United States and Canada. Their harvesting technique is ecologically sound in that only the upper part of the stem is removed, thus allowing the remaining portion of the plant to develop new stems or "heads." Historically, the peyoteros have visited the populations only rarely, allowing the plants to regenerate, but this is not the case today. Although peyote is widespread throughout northern Mexico and parts of Texas, its distribution in the United States is limited mostly to privately owned fenced areas along the Rio Grande.

As many as a million tops of the plants are harvested for use in the peyote ceremony each year, thus creating a severe demand on the populations of peyote in southern Texas. The supply of the cactus in the United States is becoming scarce because not all populations are available for periodic harvest. Some landowners have erected high fences and introduced exotic game animals, creating game ranches. Anyone, often including peyoteros, is strictly prohibited from coming onto their property unless they have paid a fee to hunt the game animals. This prohibition also includes Native Americans, who wish to go to the "peyote gardens" to collect plants for their personal use (Anderson 1995). An additional problem is that other ranchers, wishing to improve grazing for their cattle, destroy the native plants, including peyote, with giant root plows in order to plant exotic grasses. Thus, more and more people want to collect tops from the small, available populations on ranches where entry is permitted and the harvesting of peyote buttons is allowed, thus creating a serious conservation crisis. A possible solution is to allow the collection of peyote in neighboring Mexico, but both Mexican and U.S. regulations prohibit this. The only other alternative is the commercial propagation of peyote, but this has not yet been tried extensively and there is some question about its legality. Unfortunately, some Native Americans believe that cultivated peyote plants are not as "good" as those from the wild.

Importance of Artificial Propagation

CITES specifically defines artificially propagated plants as those that are grown from seeds, cuttings, or propagules



Figure 8.4. Drying tops of the peyote cactus (*Lophophora williamsii*).

under "controlled conditions" (Oldfield 1997). The stock or source of these artificially propagated plants has been established and is maintained in such a way that the survival of the species in the wild is not adversely affected. Such propagation programs should operate so that the stock organisms can be maintained indefinitely. The Convention of CITES specifically states that artificially propagated Appendix I plants (Table 8.3) may be treated in exactly the same way as Appendix II plants, which in many countries means that they are treated as non-CITES plants. However, most countries require some documentation on the origin of the plants. Unfortunately, in many cases this documentation is both expensive and extensive, which discourages many nursery operators from propagating Appendix I species.

Clearly, the impact of illegal collecting on wild populations of cacti could be greatly reduced if large numbers of quality plants were made available in the trade at a reasonable cost. Most hobbyists want to have specimens of a certain cactus, and they are willing to purchase well-grown artificially propagated plants because they know that they are both protecting the wild populations and are getting plants that have a better chance of survival in cultivation. However, there will always be a few individuals who feel they must have plants from the field. One of the most important conservation actions that can be taken is for CITES and other government agencies to encourage and facilitate the artificial propagation of Appendix I cacti.

CITES

CITES is the primary international legislation that deals with the conservation of plants and animals; it now has over 130 member countries. CITES regulates trade in threatened wild species, placing them in one of three appendices. Those species listed in Appendix I (Table 8.3) are considered to be at serious risk due to international trade; thus, trade in these organisms between signatory countries is banned. Appendix II lists those species that may be threatened by excessive amounts of trade, but for which trade is permitted with appropriate licenses, monitoring, and certain controls; all cacti not in Appendix I are listed in Appendix II. Appendix III is used by countries that

want to control trade in certain plant or animal species that are not currently in either of the other appendices. CITES appendices are amended by agreement of member countries at the biennial Conference of the Parties, which usually follows the consideration of detailed proposals that have been submitted by one or more members. Thus, changes to the listings in the appendices do occur, though the process is cumbersome. For example, *Leuchtenbergia principis* was originally listed in Appendix I, but because research showed that clearly it was not threatened with immediate extinction, it was transferred to Appendix II. Some cacti presently listed in Appendix I may not be as severely threatened as some that are not on the list, but only detailed research and extensive paperwork can make these changes.

CITES is implemented through laws and administrative procedures of member countries, as the actual Convention provides only the framework for implementation. International cooperation between member countries is essential. Each country has Scientific and Management Authorities that are responsible for implementing the Convention. In the United States, for example, these authorities are within the U.S. Fish and Wildlife Service. Standardized implementation of CITES and national regulations, especially among plants, is spotty at best. Bureaucratic red tape and regulations can inhibit the effective implementation of the CITES regulations. For instance, artificially propagated CITES plants are regulated by massive amounts of regulation and heavy financial burdens on the growers. Also, CITES was established to regulate the trade of threatened plants and animals, but legislative restrictions have created bureaucracies for legitimate scientific research. Researchers at the Desert Botanical Garden received the appropriate collecting and export permits to do field work in Peru and to collect a specific number of research specimens, but someone mistakenly reduced the number of plants that could be exported. Upon the arrival of the shipment into the United States, the inspector confiscated the "extra" plants. Although the export permit was eventually corrected by Peruvian authorities, U.S. authorities would not accept the corrected forms because they were on the wrong letterhead. The collection data were not allowed to accompany the confiscated plants, so their scientific value was lost.

Distinctions should be made between scientists doing research on cacti and those trading in these plants. Of course, scientists, like everyone else, are subject to the laws of whatever country in which they are working. Indeed, CITES has made some provision for facilitating research, as institutions may apply for permits and register with the CITES Secretariat as Institutions for Scientific Exchange. These permits authorize the non-commercial shipment of legally acquired specimens between registered institutions. The system can work well, but unfortunately some countries have few, if any, registered scientific institutions. Research is a critically important part of plant conservation, for rare plants must be understood so they may be appropriately protected, and cumbersome regulations and permit procedures can frustrate this endeavor.

The Convention on Biological Diversity

In 1992, 153 countries signed the Convention on Biological Diversity, with the objectives being "the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources" (Oldfield 1997). One of the most important aspects of this Convention is that member countries are required to identify those components of biological diversity important for both conservation and sustainable use. The Convention also requires the establishment of protected areas and the passing of appropriate legislation to protect those organisms found to be threatened. This Convention certainly contains appropriate elements for assisting conservation groups and agencies in implementing programs to protect threatened organisms, including cacti, and by helping them identify threatened species and developing measures to protect them.

In situ *and* ex situ *Conservation*

Even with agreement that threatened organisms need to be conserved and programs need to be developed to ensure their perpetuation, the ideal solutions may not be attainable. Two different approaches to the conservation of organisms are *in situ* and *ex situ* conservation. *In situ* conservation is simply protecting wild plants and animals in their natural habitats. Clearly, this is the best insurance that rare and threatened species will have a long-term chance of survival. Usually *in situ* conservation involves setting aside areas and establishing legal protections, such as those found in nature preserves, national parks, and protected private lands. It may also include habitat restoration and even the reintroduction of organisms. The U.S. Endangered Species Act provides protection for certain "critical habitats" defined as being essential for the long-term conservation of the threatened or rare species, including cacti. *Ex situ* conservation is a second level of protecting rare and endangered plants away from their natural habitats.

State and national parks, preserves, and monuments are significant regions in which threatened cacti can be protected. Three national parks or preserves in the western

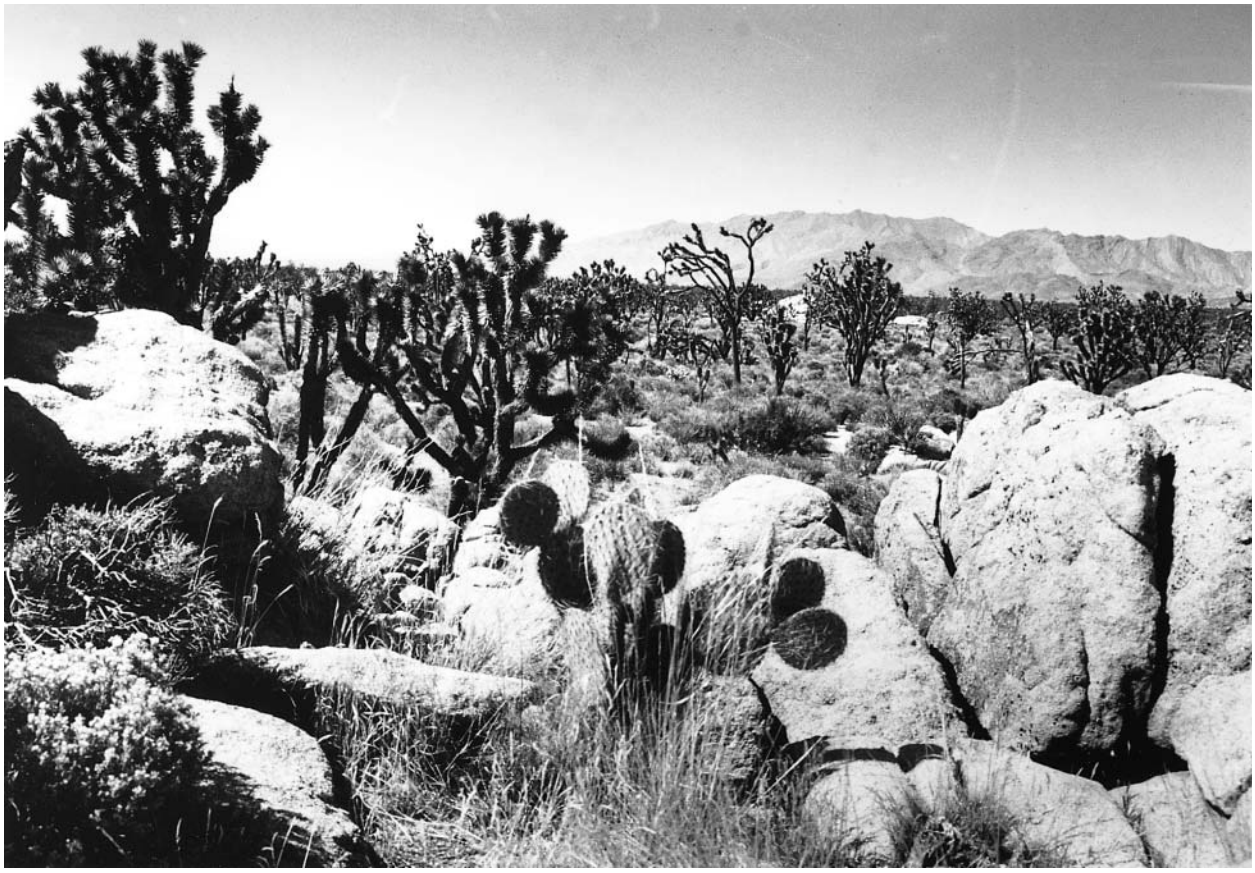


Figure 8.5. Mojave Natural Preserve Desert National Park in California.

United States have significant numbers of cacti: Joshua Tree National Park in California; Mojave Natural Preserve Desert, also in California (Fig. 8.5); and Big Bend National Park in Texas. Arizona has two national monuments specifically set aside to protect cacti: Saguaro National Monument and Organ Pipe Cactus National Monument. A significant conservation effort in South America is Pan de Azúcar National Park in Chile, in which important cacti of the Atacama Desert are protected. Although the Galápagos Islands of Ecuador are commonly thought of as having unusual animals, the Archipelago also has many remarkable species of plants, including cacti, that are protected through its status as a national park (Fig. 8.6). Mexico has established several preserves for the protection of cacti: Pinacate Reserve in Sonora, Mapimí Nature Reserve in Chihuahua, Cañon de Huasteco in Nuevo León, Parque Internacional del Río Bravo also in Nuevo León, and Isla Cedros Sanctuary in Baja California.

Private owners of land containing threatened cacti may also knowingly or unknowingly protect the native plants by prohibiting access. The Trans Pecos Heritage Association in west Texas has no conservation agenda in prohibiting access to its vast ranches; it simply does not want trespassers of any kind on its properties. Some of these ranches have populations of rare cacti, such as *Echinocereus viridiflorus* subsp. *davisii,* which are protected from collectors by the trespassing regulations. On the other hand, researchers are often prohibited from studying the plants as well. The Nature Conservancy consciously purchases tracts of land for the protection of wild species, and often this land remains in private ownership.

Despite national and local efforts to set aside critical habitats containing rare or threatened species, some people will still trespass and illegally remove plants, such as cacti, and thus adversely affect the long-term future of the populations. Both Saguaro National Monument and Big Bend National Park have suffered losses in their cacti populations from illegal activities.

Ex situ conservation is the cultivating of rare and threatened plants "away from danger" in botanic gardens and other places that are not the natural habitats of the plants involved. This type of conservation is clearly not as



Figure 8.6. Forest of *Opuntia echios* var. *barringtonensis* in the Galápagos Islands, Ecuador.

effective as the *in situ* conservation of wild populations, but the latter may be impossible because of habitat fragmentation and destruction, political pressures against conservation, legal prohibitions, bureaucratic obstacles, overcollection, and inaccessibility because of private ownership. Thus, *ex situ* conservation may be the only viable alternative in protecting and perpetuating a threatened plant. Effective *ex situ* conservation requires careful documentation, the propagation of sufficient numbers of individuals to ensure some degree of genetic diversity, and the prevention of diseases. Botanic gardens, such as the Desert Botanical Garden (Phoenix, Arizona), the Huntington Botanical Garden (San Marino, California), the Jardín Botanico del Instituto de Biologia de Universidad Nacional Autónoma de México (UNAM) in Mexico City, the Exotic Garden of Monaco, and the Zürich Succulent Collection in Switzerland are examples of gardens emphasizing the collection and growing of cacti. Other examples of *ex situ* conservation of cacti are private collections and some commercial nurseries. An example of the former is the Jardín Botanico Tropical "Pinya de Rosa" near Barcelona, Spain, which was founded by Fernando Riviere de Caralt and is now operated by his family. Steven Brack's Mesa Garden in Belen, New Mexico, is an excellent example of a commercial business that propagates and sells documented materials obtained from legally collected stock plants. These plants provide additional specimens for both hobbyists and botanic gardens. Seed banks are also important in *ex situ* plant conservation, but few contain more than just a small fraction of cactus species. The exception is the seed collection of the Desert Botanical Garden, which has seeds of several hundred cactus species.

Conclusions and Future Prospects

Although cacti inhabit a wide diversity of climatic regions and ecosystems throughout the New World, approximately half of all known species of cacti occur in four geographical regions, or centers of diversity. Among the four centers of diversity, the geographical region comprising Mexico and the southwestern United States contains the greatest concentration of species and the most endemic genera. In this regard, cacti have been the subjects of few allozyme surveys, and therefore relatively little information is available on the extent and distribution of biodiversity within individual species. Strategies for the conservation of rare or threatened cacti would be aided by more information on the extent of genetic variation within their populations. Kay and John (1996) have recommended studies of each rare or threatened species to discern the extent and distribution of genetic diversity. Their rationale for the recommendation was that inferences from presumably similar ecological situations appear to be inapplicable. This would be impractical for all rare or threatened cacti because of time and cost constraints. Gray (1996) reviewed the literature on genetic diversity in natural plant populations and concluded that genetic diversity in most plant species extends along the axis of habitat variability. Based on this finding, Gray (1996) proposed that, in the absence any genetic diversity data, as many populations as feasible across the species' entire geographic range should be conserved, protected *in situ,* or sampled for *ex situ* collections.

The amount of genetic diversity within a plant species is ultimately limited by the effective size of the populations. Wild species lose genetic diversity due to reductions in effective population size or population fragmentation. How reduced genetic diversity actually affects populations of wild cacti is not known and requires study. With regard to cultivated cacti, information on the genetic diversity of *Hatiora* and *Schlumbergera* is available but less is known about biodiversity of other economically important cacti. Efforts should therefore be made to estimate the genetic

variation present in germplasm collections of other cultivated cacti. The economically important cacti and their wild relatives should receive a high priority for conservation efforts. Germplasm of cultivated cacti and their near relatives should be collected and preserved *ex situ.* Seeds should be collected from several populations throughout the species' natural ranges. Further work may be needed to devise protocols for the long-term storage of seeds, pollen, and vegetative material.

The present is a critical period with regard to the future of cactus conservation, and the outlook is grim. It will be impossible to halt—or even slow down—habitat destruction as long as the human population grows at its current rate, especially in Latin America. Urban areas will expand and marginal land will be converted to farmland. Illegal collecting will continue. Hopefully, the efforts of national societies and the International Organization for Succulent Plant Study (IOS) to educate its members—and the public as a whole—may gradually produce a better understanding of the need for cactus conservation. Some national cactus and succulent organizations have already done a great service to conservation in prohibiting the entering of field-collected plants in sanctioned shows and competitions. Several commercial nurseries are also providing excellent plants for hobbyists.

CITES and the implementation of its regulations has been and will continue to be effective in controlling trade and its impact on wild populations, but excessive bureaucracy will frustrate and discourage many people from cooperating fully. Hopefully, CITES and the many governmental agencies concerned with conservation will streamline their permitting procedures. A number of projects were proposed in the Cactus and Succulent Action Plan (Oldfield 1997). Funding is necessary for extensive field work and monitoring so that the rare and threatened cacti may be better understood. More knowledge will enable researchers and others to manage and protect wild populations for the foreseeable future. Cacti are amazing plants and extensive conservation efforts are certainly justified. Cooperative effort among researchers, conservationists, and hobbyists is required to ensure that wild populations of cacti will continue to exist.

Literature Cited

Anderson, E. F. 1995. The "peyote gardens" of south Texas: A conservation crisis. *Cactus and Succulent Journal (U.S.)* 67: 67–73.

Anderson, E. F. 1996. *Peyote: The Divine Cactus,* 2nd ed. University of Arizona Press, Tucson.

Anderson, E. F. (compiler). 1997. CITES Project S-53: Population Study on Rare Mexican Cacti. A report to CITES on a three-year monitoring and study project. Desert Botanical Garden, Phoenix, Arizona.

Anderson, E. F., and R. Schmalzel. 1997. Joint Task Force Six Lloyd's Mariposa Cactus Survey (*Sclerocactus* [*Neolloydia*] *mariposensis*). A report to JTF-6 on a three-year study of this rare cactus of Texas and Mexico. Desert Botanical Garden, Phoenix, Arizona.

Anderson, E. F., and S. M. Skillman. 1984. A comparison of *Aztekium* and *Strombocactus* (Cactaceae). *Systematic Botany* 9: 42–49.

Anderson, E. F., N. P. Taylor, and S. Arias Montes. 1994. *Threatened Cacti of Mexico.* Royal Botanic Gardens, Kew, United Kingdom.

Barbier, E. B. 1997. Ecological economics, uncertainty and implications for policy setting priorities for biodiversity conservation. In *Investing in Biological Diversity: The Cairns Conference (OECD Proceedings).* Organization for Economic Co-operation and Development, Paris. Pp. 115–140.

Barthlott, W. 1983. Biogeography and evolution in neo- and paleotropical Rhipsalinae (Cactaceae). In *Dispersal and Distribution* (K. Kubitzki, ed.). Sonderbände des naturwissenschaftlichen Vereins in Hamburg 7. Verlag Paul Parey, Hamburg. Pp. 241–248.

Barthlott, W., and D. R. Hunt. 1993. Cactaceae. In *The Families and Genera of Vascular Plants. Vol. II: Flowering Plants* (K. Kubitzki, ed.). Springer-Verlag, Berlin. Pp. 161–197.

Barthlott, W., G. Rauer, P. L. Ibisch, M. von den Driesch, and W. Lobin. 2000. Biodiversität und botanische Gärten. In *Botanische Gärten und Biodiversität* (Bundesamt für Naturschutz, Bonn, ed.). Landwirtschaftsverlag, Munich. Pp. 1–24, 69–70.

Boyle, T. H. 1997. The genetics of self-incompatibility in the genus *Schlumbergera* (Cactaceae). *Journal of Heredity* 88: 209–214.

Brown, A. H. D., and J. D. Briggs. 1991. Sampling strategies for genetic variation in ex-situ collections of endangered plant species. In *Genetics and Conservation of Rare Plants* (D. A. Falk and K. E. Holsinger, eds.). Oxford University Press, New York. Pp. 99–122.

Chessa, I., G. Nieddu, P. Serra, P. Inglese, and T. La Mantia. 1997. Isozyme characterization of *Opuntia* species and varieties from Italian germplasm. *Acta Horticulturae* 438: 45–52.

del Castillo, R. F. 1986. La selección natural de los sistemas de cruzamiento en *Opuntia robusta.* Master's Thesis, Colegio de Postgraduados, Chapingo, Mexico.

de Nettancourt, D. 1977. *Incompatibility in Angiosperms.* Monographs on Theoretical and Applied Genetics 3. Springer-Verlag, Berlin.

Doebley, J. 1989. Isozymic evidence and the evolution of crop plants. In *Isozymes in Plant Biology* (D. E. Soltis and P. S. Soltis, eds.). Dioscorides Press, Portland, Oregon. Pp. 165–191.

Ellstrand, N. C., and M. L. Roose. 1987. Patterns of genotypic diversity in clonal plant species. *American Journal of Botany* 74: 123–131.

Fleming, T. H., S. Maurice, S. L. Buchmann, and M. D. Tuttle. 1994. Reproductive biology and relative male and female fitness in a trioecious cactus, *Pachycereus pringlei* (Cactaceae). *American Journal of Botany* 81: 858–867.

Fleming, T. H., M. D. Tuttle, and M. A. Horner. 1996. Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran Desert columnar cacti. *The Southwestern Naturalist* 41: 257–269.

Frankel, O., A. H. D. Brown, and J. J. Burdon. 1995. *The Conservation of Plant Biodiversity.* Cambridge University Press, Cambridge.

Ganders, F. R., and H. Kennedy. 1978. Gynodioecy in *Mammillaria dioica* (Cactaceae). *Madroño* 25: 234.

Gates, H. E. 1932. *Lophocereus* in lower California. *Cactus and Succulent Journal (U.S.)* 3: 136–137.

Given, D. R. 1994. *Principles and Practice of Plant Conservation.* Timber Press, Portland, Oregon.

Grant, V., and K. A. Grant. 1979. The pollination spectrum in the southwestern American cactus flora. *Plant Systematics and Evolution* 133: 29–37.

Grant, V., and P. D. Hurd. 1979. Pollination of the southwestern opuntias. *Plant Systematics and Evolution* 133: 15–28.

Gray, A. 1996. Genetic diversity and its conservation in natural populations. *Biodiversity Letters* 3: 71–80.

Hamrick, J. L. 1989. Isozymes and the analysis of genetic structure in plant populations. In *Isozymes in Plant Biology* (D. E. Soltis and P. S. Soltis, eds.). Dioscorides Press, Portland, Oregon. Pp. 87–105.

Hamrick, J. L., and M. J. W. Godt. 1989. Allozyme diversity in plant species. In *Plant Population Genetics, Breeding, and Genetic Resources* (A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir, eds.). Sinauer Associates, Sunderland, Massachusetts. Pp. 43–63.

Hamrick, J. L., and M. J. W. Godt. 1996. Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 351: 1291–1298.

Hoffmann, M. T. 1992. Functional dioecy in *Echinocereus coccineus* (Cactaceae): Breeding system, sex ratios, and geographic range of floral dimorphism. *American Journal of Botany* 79: 1382–1388.

Hunt, D. R. 1992. *CITES Cactaceae Checklist.* Royal Botanic Gardens and International Organization for Succulent Study (IOS), Kew, United Kingdom.

Innes, C., and C. Glass. 1991. *Cacti.* Portland House, New York.

IUCN/SSC Criteria Review Working Group. 1999. IUCN red list criteria review provisional report: Draft of the proposed changes and recommendations. *Species* 31/32: 43–57.

Kay, Q., and R. John. 1996. Patterns of variation in relation to the conservation of rare and declining plant species. In *The Role of Genetics in Conserving Small Populations* (T. J. Crawford, T. Spencer, D. Stevens, T. E. Tew, M. B. Usher, and J. Warren, eds.). Joint Nature Conservation Committee, Peterborough, United Kingdom.

Meier, E. 1995. Easter cacti (*Rhipsalidopsis;* Cactaceae). *Haseltonia* 3: 10–24.

Murawski, D. A., T. H. Fleming, K. Ritland, and J. L. Hamrick. 1994. Mating system of *Pachycereus pringlei:* An autotetraploid cactus. *Heredity* 72: 86–94.

Nei, M. 1973. Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences U.S.A* 70: 3321–3323.

Oldfield, S. (compiler). 1997. *Cactus and Succulent Plants: Status Survey and Conservation Action Plan.* IUCN/SSC Cactus and Succulent Specialist Group. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, and Cambridge, United Kingdom.

O'Leary, M. C., and T. H. Boyle. 1999. Cultivar identification and genetic diversity within a *Hatiora* (Cactaceae) clonal germplasm collection. *Journal of the American Society for Horticultural Science* 124: 373–376.

O'Leary, M. C., and T. H. Boyle. 2000. Diversity and distribution of isozymes in a *Schlumbergera* (Cactaceae) clonal germplasm collection. *Journal of the American Society for Horticultural Science* 125: 81–85.

Olesen, J. M., and S. K. Jain. 1994. Fragmented plant populations and their lost interactions. In *Conservation Genetics* (V. Loeschcke, J. Tomiuk, and S.K. Jain, eds.). Birkhäuser Verlag, Basel. Pp. 417–426.

Olmstead, R. G. 1986. Self-incompatibility in light of population structure and inbreeding. In *Biotechnology and Ecology of Pollen* (D. L. Mulcahy, G. B. Mulcahy, and E. Ottoviano, eds.). Springer-Verlag, New York.

Parfitt, B. D. 1985. Dioecy in North American Cactaceae. *Sida* 11: 200–206.

Parker, K. C., and J. L. Hamrick. 1992. Genetic diversity and clonal structure in a columnar cactus, *Lophocereus schottii. American Journal of Botany* 79: 86–96.

Petit, S., and L. Pors. 1996. Survey of columnar cacti and carrying capacity for nectar-feeding bats on Curaçao. *Conservation Biology* 10: 769–775.

Porsch, O. 1938. Das Bestäubungsleben der Kakteenblüte. *Jahrbuch der Deutsche Kakteen-Gesellschichte* I: 1–80.

Porsch, O. 1939. Das Bestäubungsleben der Kakteenblüte. *Jahrbuch der Deutsche Kakteen-Gesellschichte* II: 81–142.

Redford, K. H., A. Taber, and J. A. Simonetti. 1990. There is more to biodiversity than tropical rain forests. *Conservation Biology* 4: 328–330.

Reid, W. V., J. A. McNeely, D. B. Tunstall, D. A. Bryant, and M. Winograd. 1993. *Biodiversity Indicators for Policy-Makers.* World Resources Institute, Washington, D.C.

Rowley, G. 1980. Pollination syndromes and cactus taxonomy. *Cactus and Succulent Journal (Great Britain)* 42: 95–98.

Sahley, C. T. 1996. Bat and hummingbird pollination of an autotetraploid columnar cactus, *Weberbauerocereus weberbaueri* (Cactaceae). *American Journal of Botany* 83: 1329–1336.

Schlindwein, C., and D. Wittmann. 1997. Stamen movements in flowers of *Opuntia* (Cactaceae) favour oligolectic pollinators. *Plant Systematics and Evolution* 204: 179–193.

Schmalzel, R., and E. F. Anderson. 1999. *Study of the Bunched Cory Cactus* (*Coryphantha ramillosa* Cutak). A report to the U.S. Fish and Wildlife Service, Washington, D.C.

Taylor, N. P. 1997. Cactaceae. In *Cactus and Succulent Plants—Status Survey and Conservation Action Plan* (S. Oldfield, compiler). International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, and Cambridge, United Kingdom. Pp. 17–20.

Uzun, I. 1997. Fruit and cladode isozymes in cactus pear. *Acta Horticulturae* 438: 45–52.

Wallace, R. S., and D. E. Fairbrothers. 1986. Isoelectrically focussed seed proteins of populations of *Opuntia humifusa* (Raf.) Raf. (Cactaceae). *Biochemical Systematics and Ecology* 14: 365–369.

Walter, K. S., and H. J. Gillett (eds.). 1998. *1997 IUCN Red List of Threatened Plants.* International Union for Conservation of Nature and Natural Resources and The World Conservation Union, Gland, Switzerland.

Wilcox, B. A. 1984. *In situ* conservation of genetic resources: Determinants of minimum area requirements. In *National Parks, Conservation, and Development: The Role of Protected Areas in Sustaining Society* (J. A. MacNeely and K. R. Miller, eds.). Smithsonian Institution, Washington, D.C. Pp. 639–647.

CHAPTER

› 9 ‹

MESOAMERICAN DOMESTICATION AND DIFFUSION

Alejandro Casas and Giuseppe Barbera

Introduction
Human-Cactus Interactions in Mesoamerica
Archaeological and Historical Evidence
Ethnobotanical Information
Domestication of Cacti
Columnar Cacti
Opuntia *Species*
Diffusion of Cacti to Other Regions of the World
Colonial Period
Spread of Platyopuntias in Europe
History of Name
Naturalization in Europe
Platyopuntias in Sicily
Expansion to Other Mediterranean Regions
Conclusions and Future Prospects
Literature Cited

Introduction

Mesoamerica, the culturally defined region from central Mexico to northwestern Costa Rica (Fig. 9.1), is one of the most important centers of domestication of plants in the world (Harlan 1975). Archaeological studies suggest that domestication of plants in this region was initiated approximately 9,600 years ago (Flannery 1986). Dressler (1953) estimated that about 100 cultivated species (e.g., maize, beans, squashes, tomatoes, avocados, and prickly pears) were domesticated by pre-Columbian cultures of Mesoamerica. Actually, ethnobotanical studies indicate that several hundred species were domesticated, some only in a beginning stage and others to advanced stages, but many have been poorly studied because they are only regionally or locally important. Apart from *Opuntia* spp. and *Hylocereus undatus,* cacti are commonly omitted from checklists of domesticated plants. Nevertheless, archaeologists have revealed that several species of *Opuntia* as well as columnar and barrel cacti were among the most important plant resources utilized by humans in prehistoric Mesoamerica (Callen 1967; Smith 1967, 1986), and ethnobotanists have documented that dozens of species of cacti are currently utilized by indigenous peoples of this



Figure 9.1. Mesoamerica and states for the Mexican part of the region (Matos 1994; Vargas 1994).

area, indicating that several species of *Opuntia* and columnar cacti are in advanced stages of domestication (Colunga 1984; Casas et al. 1997a, 1999a, b).

Domestication is an evolutionary process resulting from the manipulation of living organisms by humans. In this process, humans select and breed phenotypes with characteristics they consider advantageous; i.e., individual plants with better qualities as food, medicine, and other uses. Other evolutionary forces, such as genetic drift, also intervene in the selection process and may be significant in small populations caused by humans due to the isolation of individual plants or resulting from perturbation and fragmentation of natural habitats or transplantation of wild individuals into human habitats. Throughout history, human migrations, displacement of human settlements, commerce, cultural exchange, as well as conquest and colonization of new areas have been accompanied by the movement of plant and animal populations (individuals and/or their propagules) from one region to another. In some cases, migration has isolated individuals from their parental populations, and the influence of artificial selection under different cultural and environmental contexts can determine particular routes of domestication. In other cases, migration has reestablished contact between variants previously separated by natural or human processes, giving rise to new combinations of genes that are available for artificial selection. Through domestication, plant populations become morphologically, physiologically, and/or behaviorally divergent from their wild ancestors (Darwin 1868; Harlan 1992). But, as in general evolutionary processes, the inherited, genetically controlled divergence can be considered a domestication process.

Domestication of plants has generally been associated with cultivation (Harlan 1992), because artificial selection more probably occurs under successive generations of harvest and propagation of the desired phenotypes. However,

domestication can also act under different forms of manipulation of wild plant populations *in situ,* including species of cacti (Casas et al. 1997b). Indeed, Mesoamerican indigenous peoples commonly practice a broad spectrum of interactions with plants (Alcorn 1984; Colunga 1984; Bye 1993; Casas et al. 1996, 1997a). Casas et al. (1996) group these forms of plant management into those occurring *in situ* (in the wild) and those occurring *ex situ.* Through interactions *in situ,* humans may take products from nature without significant perturbations, but they may also alter the structure of plant populations by increasing the quantity of target species or particular phenotypes. The main interactions *in situ* are: (1) gathering, which is the taking of useful plant products directly from natural populations; (2) tolerance, including practices directed to maintain, within human-made environments, useful plants already occurring there; (3) enhancement, directed to increase the population density of useful plant species, including the sowing of seeds or the intentional propagation of vegetative structures in places occupied by wild plant populations; and (4) protection, which includes conscious activities, such as the elimination of competitors or predators, fertilization, and pruning to safeguard critical wild plants. Plant management *ex situ* includes interactions taking place outside natural populations, in habitats created and controlled by humans, including: (1) transplantation of entire individuals and (2) sowing and planting of sexual or vegetative propagules (Casas et al. 1996, 1997a,b).

Variation among the species composing a plant community or the individuals forming a population, their differences in quality as useful resources, and the selective attitude of humans in taking advantage of some species and particular individuals and not others are the most important principles in artificial selection of plants. Ethnobotanical studies in Mesoamerica have revealed that this attitude is common among indigenous peoples and that it occurs under different interactions between humans and plants, not only under cultivation. In gathering, people usually make choices among individual plants based on their quality as a food, such as flavor, size, color, and presence of toxic substances (Casas et al. 1996, 1997a, 1999b). This selection may give rise to other types of interaction involving domestication. When they are found during the clearing of forest areas, the edible wild plant species and the preferred variants may be spared, enhanced, and/or protected *in situ,* whereas those species and variants whose edible parts are not preferred by people are eliminated. Over the long term such selective attitudes may modify vegetation patches in which the phenotypes desirable to humans have a better opportunity to be components of the community, and the selected components may increase their frequency in populations, another facet of plant domestication.

This chapter examines cultural and biological aspects related to the use and management of cacti among peoples of Mexican Mesoamerica and analyzes how domestication is occurring in some species. Comparisons of morphology between wild and manipulated populations of *Opuntia* and *Stenocereus* species are used to illustrate patterns of artificial selection and evolutionary trends resulting from domestication under different forms of management. This information is discussed to determine how domestication might be occurring in other cacti. The diffusion of cacti, especially platyopuntias, into other regions of the world is reviewed to examine trends in domestication of these species outside of Mesoamerica.

Human-Cactus Interactions in Mesoamerica

Archaeological and Historical Evidence

Mexico is apparently the richest area for cactus species in the world (Bravo-Hollis 1978). Cacti are among the main components of the tropical deciduous and thorn-scrub forests of subhumid tropics as well as arid and semiarid zones, which cover nearly two-thirds of the country (Toledo and Ordóñez 1993). Archaeological studies in the Tehuacán Valley, Puebla (MacNeish 1967), and at Guilá Naquitz, Oaxaca (Flannery 1986), suggest that the region was inhabited by humans probably from 14,000 years before present (BP) and have found there the oldest evidence of plant domestication in the New World. Since ancient times, people of this area have used a broad spectrum of plant and animal species as resources, and cacti have been among the most important because of their abundance, diversity, and edible parts.

Prehistoric human colonization of the Mexican territory most likely occurred in a north-south direction. According to this theory, people arrived from northern Aridoamerica, the vast territory occupied by the Sonoran and Chihuahuan deserts, where prehistoric bands of hunter-gatherers interacted for a long time with cacti as main resources. Inhabitants of the prehistoric Mesoamerica exhibited a strong cultural utilization of cacti, developed by their ancestors from Aridoamerica and their own experience with local arid and semiarid environments. Later on, continual migrations of peoples (including the Aztecs) from northern Mexico into Mesoamerica progressively reinforced the development of cactus utilization among the great civilizations; this utilization persists until today.

TABLE 9.1
Archaeological remains of cacti in caves of the Tehuacán Valley (Puebla, P) and Guilá Naquitz (Oaxaca, O) in central Mexico

Species	Phase, with radiocarbon date (years before present, BP) in parentheses								
	Ajuereado (14,000–8,800)	*El Riego (8,800–7,000)*	*Coxcatlán (7,000–5,400)*	*Abejas (5,400–4,300)*	*Purrón (4,300–3,500)*	*Ajalpan (3,500–2,800)*	*Sta. María (2,800–2,150)*	*Palo Blanco (2,150–1,300)*	*Venta Salada (1,300–500)*
Cephalocereus columna trajani		P	P			P	P		
Echinocactus platyacanthus		P						P	
Escontria chiotilla			P					P	
Ferocactus flavovirens								P	P
Myrtillocactus geometrizans		P	P						P
Opuntia spp.	P, O	P, O	P, O	P, O	P, O	P, O	P, O	P, O	P, O
Pachycereus hollianus		P	P	P					
P. weberi		P	P	P			P	P	
Stenocereus stellatus				P				P	

Adapted from MacNeish (1967) and Smith (1967, 1986).

Smith (1967) reported remains of nine cactus species (Table 9.1) from archaeological excavations of prehistoric Mesoamerican sites in caves of the Tehuacán Valley. For caves at Guilá Naquitz, Smith (1986) reports stems, fruits, and seeds of *Opuntia* species in almost all of the stratigraphic zones studied, from nearly 12,000 years BP, as well as a gumball that could have come from a columnar cactus. Callen (1967) identified the following types of cactus remains in human coprolites of Tehuacán: (1) "*Opuntia,*" which might represent some of the 18 species of this genus existing in the region (Arias et al. 1997); (2) "*Lemaireocereus,*" which might represent some of the 13 species of columnar cacti of the genera *Escontria, Myrtillocactus, Pachycereus, Polaskia,* and *Stenocereus* (Casas et al. 1999a); and (3) "cactus tissue," from unidentified cacti. Callen (1967) further found that in the earliest coprolites from the El Riego phase (8,500–7,000 years BP), these types of cactus remains were a part of a wild food diet, along with *Setaria* spp. seeds, pochote (*Ceiba parvifolia*) roots, maguey (*Agave* spp.) leaves, and meat. In the Coxcatlán phase (7,000–5,500 years BP), stem tissue and fruits of "*Opuntia*" and "*Lemaireocereus*" were equally dominant materials. In the Abejas (5,500–3,300 years BP), Ajalpan (3,500–2,900 years BP), Santa María (2,900–2,200 years BP), Palo Blanco (2,200–1,300 years BP), and Venta Salada (1,300–460 years BP) phases, findings suggest that consumption of "*Lemaireocereus*" stem tissue, fruits, and seeds were more important than products of "*Opuntia*"; and during the Ajalpan and Santa María phases, "*Lemaireocereus*" was the principal plant constituent of human diets.

The importance of cacti in Mesoamerican cultures can be recognized in pre-Columbian codices, which contain many toponymic glyphs referring to the names of cacti or their parts. Among the most famous are *Tenochtitlán* ("place of stony prickly pears" in Náhuatl), the original name of Mexico City, and *Nochistlán* ("place of prickly pears" in Náhuatl), in the state of Oaxaca. Historical information on utilization of cacti can be found in *La Historia General y Natural de las Indias,* published by Oviedo y Valdés in 1535. The Barberini Codex from 1552 (De la Cruz and Badiano 1964) includes information on medicinal utilization of *Tlatocnochtli,* a species of *Opuntia,* and a description of *Teonochtli,* identified as *Stenocereus* sp. by Bravo-Hollis (1978). The *Florentino Codex* (Sahagún 1970) contains a section dedicated to the description of the "diversity of tunas," which includes a list of variants of *Opuntia* species and their uses as edible fruits and stems. Estrada (1989) identified *Cacanochnopalli* (a Náhuatl term) as *O. megarhiza, Tecolnochnopalli* as *O. streptacantha, Uitzocuitlapalli* as *Aporocactus flagelliformis, Nopalxochitl* as

Epiphyllum ackermanii, Teonochtli as *Hylocereus undatus, Peyotl* as *Lophophora williamsii* (now commonly known as "peyote"), as well as several types of *Tecomitl* as *Mammillaria, Echinocactus,* and *Ferocactus* species. The *Florentino Codex* also includes information on two columnar cacti, one of them called *Netzolli,* which is probably *Escontria chiotilla,* and *Teunochtli,* which could be a species of *Stenocereus* (Casas et al. 1999a). The books of Francisco Hernández in the 16th century describe several species of cacti utilized as medicine, among them several species of *Opuntia,* two columnar cacti identified as *Myrtillocactus geometrizans,* and a possible *Stenocereus* species called *Teonochtli* (Hernández 1959). The *Geographic Relations of the XVI Century* described the cultivation of *Opuntia* species for the production of cochineal and contains a reference to the columnar cactus *Teonochtli,* the "Relation of Acatlán" (Acuña 1985). Based on these sources, cacti were clearly utilized as food (fruits, young stems, and in some cases the flowers and seeds) and medicine (fruits, stems, and roots).

In the 16th century, Oviedo y Valdés (1535) and Sahagún (1985) described how the harvest of fruits of *Opuntia* spp. and columnar cacti was crucial for subsistence of some pre-Columbian and post-Conquest peoples from northern and central Mexico. For example, indigenous people migrated during the summer from the coast of the Gulf of Mexico to the highlands of the northern plateau, looking for the fruits of platyopuntias. In this region, people stayed for two months, migrating from place to place consuming fruits.

Smith (1967) considered that species of *Opuntia* could have been among the first plants subject to human manipulation in the Tehuacán Valley, but no archaeological evidence exists. Apparently, *Opuntia* was cultivated in the 16th century for the production of cochineal (*Opuntia ficus-indica, O. tomentosa* var. *hernandezii,* and *Nopalea cochenillifera*). However, cultivation of *Opuntia* and columnar cacti for the production of fruits, as currently occurs, was not clearly recorded. The only document that indicates such cultivation is the book of Sahagún (1985), in which the wild variants are distinguished from others (presumably cultivated). This omission could be because the Spaniards did not consider fruits of cacti as important resources and therefore did not describe them, as was the case for many other plants cultivated by natives (Casas et al. 1999a). Such omission could also be explained if cultivation of these plants started more recently. Further studies can provide information on the changes of cacti under domestication, which would be helpful to estimate the antiquity of cactus domestication.

Ethnobotanical Information

According to the compendium of the Cactaceae of Mexico by Bravo-Hollis (1978; Bravo-Hollis and Sánchez-Mejorada 1991), about 850 cactus species occur within the Mexican territory and 420 in the Mesoamerican region. Ethnobotanical studies in the region have documented a total of 118 cacti species utilized by indigenous peoples (Table 9.2). Useful cacti include *Opuntia* species, epiphytes, as well as columnar, spherical, barrel, and shrubby cacti. Among the columnar cacti, nearly half of the species are uncultivated giant columnar cacti, some about 15 m tall, with slow vegetative growth, which flower only after decades (Casas et al. 1999a). However, 23 species of columnar cacti (Table 9.2) are 2 to 8 m high. They grow faster than the giant columnar cacti, and flower 6 to 8 years after seed germination (2–4 years after vegetative propagation); most of them reproduce vegetatively and are cultivated.

Cacti are used mainly for their fruits, which may be consumed both fresh and dried and are used to prepare jams (Table 9.2). With the exception of subfamily Pereskioideae, fruits of nearly all species of cacti are consumed by people (Bravo-Hollis 1978). Fruits of 83 species (Table 9.2) are the most commonly consumed, and it is possible to distinguish: (1) species producing sweet juicy fruits, which are "good quality fruits" and are commonly harvested; (2) species whose fruits are of "regular quality" and are collected only occasionally, because of the scarcity of individual plants or populations, tall branches, long or abundant spines, or lack of tastiness; and (3) species whose fruits do not contain juicy pulp and are consumed only during food scarcity. The main groups of cacti producing edible fruits are columnar cacti and *Hylocereus* species with fruits called *pitayas* and *pitahayas,* respectively (Chapter 11); some *Mammillaria* species with fruits called *chilitos;* and, most important, *Opuntia* species (Chapter 10), whose sweet fruits are called *tunas* and consumed fresh, and whose sour fruits are called *xoconoztles* (from the Náhuatl *xocotl,* meaning sour, and *nochtli,* prickly pear) and are utilized as greens, condiments (boiled or fried), or as an ingredient for several other dishes. Colunga (1984) identified as *xoconoztles* variants of the species *Opuntia joconstle, O. lasiacantha, O. leucotricha,* and *O. streptacantha* as well as the red variant *jitomatilli* of *O. megacantha,* which is utilized as a substitute for tomato, and the variant *brevas* of *Opuntia robusta* var. *robusta,* whose peel is consumed fried, resembling French fried potatoes.

From the useful species of cacti reported, the stems of 62 species are cut and fed (after removal of the spines) as fodder to domestic donkeys, cows, and goats (Table 9.2).

TABLE 9.2
Species of cacti from Mexican Mesoamerica

Species	Uses[a]	Type[b]	Status[c]	Mexican states[d]	Reference
Acanthocereus pentagonus	1**, 5, 7, 8	Shr	w	7, 16, 19, 21	Caballero (1992)
A. subinermis	5, 7	Shr	w, c	7, 16	Casas et al. (2001)
Aporocactus flagelliformis	8, 9	Shr	c	General	Bravo-Hollis (1978)
Backebergia militaris	1, 2	G col	w	9, 15	Casas et al. (1999a)
Cephalocereus apicicephalium	1, 2	G col	w	16	"
C. chrysacanthus	1*, 2	G col	w	14, 16	"
C. collinsii	1*, 2	S col	w	16	"
C. columna-trajani	1*, 2, 6	G col	w	14	"
C. guerreronis	1, 2	S col	w	15	"
C. nizandensis	1, 2	G col	w	16	"
C. palmeri var. *sartorianus*	1*, 2	G col	w	16	"
C. purpusii	1, 2	S col	w	9	"
C. quadricentralis	1, 2	S col	w	16	"
C. senilis	9	G col	w, c	6, 7	Bravo-Hollis (1978)
C. totolapensis	1, 2	G col	w	16	Casas et al. (1999a)
Coryphantha radians	2, 5	Sph	w	4, 5, 6, 16	Pennington (1963); Bravo-Hollis (1978)
C. pallida	2, 9	Sph	w	14, 16	Casas et al. (2001)
Echinocactus platyacanthus	5	Bar	w, m	4, 5, 6, 14, 16	Del Castillo and Trujillo (1991); Casas et al. (2001)
E. cinerascens	1, 8	Shr	w	4, 5, 6, 10, 11	Sánchez Mejorada (1982)
E. pulchellus	5	Shr	w	6, 14	Casas et al. (2001)
Escontria chiotilla	1**, 2, 3, 4, 5, 7, 11	S col	w, m	9, 14, 15, 16	Casas, et al. (1999a)
Ferocactus flavovirens	2	Sph	w	14, 16	Casas et al. (2001)
F. haematacanthus	1, 2	Sph	w	7, 14	Bravo-Hollis (1978); Casas et al. (2001)
F. histrix	1, 5	Bar	w	4, 5, 6, 14	Del Castillo and Trujillo (1991)
F. latispinus	1, 2, 5, 9	Sph	w	5, 6, 10, 11, 14, 16	Sánchez-Mejorada (1982); Casas et al. (2001)
F. macrodiscus	1, 5	Sph	w	4, 5, 14, 16	Pennington (1963); Casas et al. (2001)
F. recurvus	5	Bar	w	14, 16	Bravo-Hollis (1978); Casas et al. (2001)
F. robustus	2	Sph	w	14, 16	Casas et al. (2001)
Heliocereus cinnabarinus	1	Ep	w, m	21	Berlin et al. (1973)
H. elegantissimus	1, 8, 9	Ep	w, m, c	10, 13, 16	Guerra (1986); Cedillo (1990)
H. speciosus	8, 9	Ep	w, c	10	Bravo-Hollis (1978)
H. schrankii	9	Ep	w, c	6, 14, 16	Casas et al. (2001)
Hylocereus ocamponis	1*	Ep	w	8, 9	A. Casas (unpublished observation)
H. purpusii	1	Ep	w, c	1, 2, 8, 9, 14, 16	Bravo-Hollis (1978); Casas et al. (2001)
H. stenopterus	1*	Ep	w	16	Bravo-Hollis (1978)
H. undatus	1**, 9	Ep	c	General	Martínez (1993)

[a]Uses: 1 = edible fruits (*regular quality, **good quality); 2 = fodder; 3 = alcoholic beverage; 4 = edible seeds; 5 = edible stems and flowers; 6 = house construction; 7 = living fences; 8 = medicine; 9 = ornamental; 10 = adhesive; 11 = fuel wood.

[b]Type: Op = *Opuntia*; Ep = epiphyte; Sph = spherical; G col = giant columnar; S col = small columnar; Bar = barrel; Shr = shrubby.

[c]Cultural status: w = wild; m = managed *in situ*; c = cultivated.

[d]Numbers for Mexican states (see Figure 9.1) are as follows: 1 = Nayarit; 2 = Jalisco; 3 = San Luis Potosí; 4 = Guanajuato; 5 = Queretaro; 6 = Hidalgo; 7 = Verzcruz; 8 = Colima; 9 = Michoacán; 10 = México; 11 = Mexico City; 12 = Tlaxcala; 13 = Morelos; 14 = Puebla; 15 = Guerrero; 16 = Oaxaca; 17 = Yucatán; 18 = Chiapas; 19 = Zacatecas.

TABLE 9.2 *(continued)*

Species	Uses	Type	Status	Mexican states	Reference
Lophophora williamsii	8	Sph	w	3, 19	Pennington (1963); Martínez (1993)
Mammillaria carnea	1, 2	Sph	w	6, 14, 15, 16	Bravo-Hollis (1978); Casas et al. (2001)
M. collina	9	Sph	w, c	7, 14, 16	Bravo-Hollis (1978); Casas et al. (2001)
M. discolor	5	Sph	w	7, 14	Bravo-Hollis (1978)
M. haageana	5, 9	Sph	w, c	7, 14, 16	Pennington (1963); Casas et al. (2001)
M. magnimamma	1**	Sph	w	7, 9 10, 11, 12, 14	Bravo-Hollis (1978)
Melocactus maxonii	5	Sph	w	16	"
M. ruestii	5	Sph	w	16,18	"
Mitrocereus fulviceps	1*, 2, 6	G col	w	14, 16	Casas et al. (1999a)
Myrtillocactus geometrizans	1**, 2, 3, 5, 7	S col	w, m	9, 15, 16	"
M. schenkii	1**, 2, 3, 5, 7	S col	w, m, c	14, 16	"
Neobuxbaumia macrocephala	1, 2, 6	G col	w	14	"
N. mezcalaensis	1**, 2, 4, 5, 6	G col	w	9, 13, 14, 15, 16	"
N. multiareolata	1, 2	G col	w	15	"
N. scoparia	1, 2	G col	w	16	"
N. tetetzo	1**, 2, 4, 5, 6	G col	w	14, 16	"
Nopalea auberi	5, 8, 9	Op	w, c	13, General	Bravo-Hollis (1978); Casas et al. (2001)
N. cochenillifera	2, 5, 8	Op	w, m, c	16, General	Pennington (1969); Bravo-Hollis (1978)
N. dejecta	2, 5	Op	c	7, 18	Bravo-Hollis (1978)
N. escuintlensis	1**	Op	w	18	"
N. lutea	1**	Op	w	18	"
N. karwinskiana	8	Op	w	9, 15, 16	Bravo-Hollis (1978); Martínez (1993)
Nopalxochia ackermanii	9	Ep	w, c	7, 16	Bravo-Hollis (1978)
N. conzatitianum	9	Ep	w, c	16	"
N. macdougallii	9	Ep	w, c	18	"
N. phyllantoides	9	Ep	w, c	7, 14	"
Opuntia amyclaea	1*, 9	Op	c	General	"
O. atropes	1, 11	Op	w, m	4, 9, 10, 13, 15	Bravo-Hollis (1978); Colunga (1984)
O. bensonii	1**	Op	w	9	Bravo-Hollis (1978)
O. crassa	1**, 11	Op	c	4, 11	Bravo-Hollis (1978); Colunga (1984)
O. decumbens	2, 5, 11	Op	w	14, 15, 16	Casas et al. (2001)
O. ficus-indica	1**, 2, 5, 8, 10, 11	Op	c	General	Bravo-Hollis (1978); Colunga (1984)
O. fuliginosa	1**, 11	Op	w, m	4, 8, 9	Colunga (1984)
O. huajuapensis	1, 2, 3, 5, 8, 9	Op	w	14, 16	Casas et al. (2001)
O. hyptiacantha	1**, 2, 11	Op	w, m	4, 10, 11	Bravo-Hollis (1978); Colunga (1984)
O. imbricata	1*, 2, 5, 8	Op	w	4, 5, 10, 11	Sánchez Mejorada (1982)
O. jaliscana	1**, 11	Op	w, m	4, 9	Bravo-Hollis (1978); Colunga (1984)
O. joconostle	1**, 11	Op	w, m, c	4, 5, 9, 10, 11	Martínez (1993)
O. kleiniae	7	Op	c	14	Arias et al. (1997)

(*continued on next page*)

TABLE 9.2 *(continued)*

Species	Uses	Type	Status	Mexican states	Reference
O. lasiacantha	1*, 2, 9, 11	Op	w, m, c	4, 10, 11, 14, 16	Bravo-Hollis (1978)
O. leptocaulis	1, 2, 5, 8	Op	w	5, 6, 14, 16	Sánchez Mejorada (1982); Felger and Moser (1983)
O. leucotricha	1**, 2, 11	Op	w, m	4, 5, 6	Bravo-Hollis (1978); Colunga (1984)
O. megacantha	1**, 11	Op	w, m, c	4	Colunga (1984)
O. nerpicolor	1*, 5	Op	w		Sánchez Mejorada (1982)
O. pilifera	1*, 2, 11	Op	w, m	14, 16	Bravo-Hollis (1978); Casas et al. (2001)
O. robusta	1**, 2, 5, 11	Op	w, m, c	4, 5, 6, 9	Bravo-Hollis (1978); Colunga (1984)
O. spinulifera	1**	Op	c	10	Bravo-Hollis (1978)
O. stenopetala	2, 8	Op	w	4, 5, 6	Sánchez Mejorada (1982)
O. streptacantha	1**, 2, 5, 3, 11	Op	w, m, c	4, 5, 6, 14, 16	Bravo-Hollis (1978); Colunga (1984)
O. tehuantepecana	1*, 5, 8	Op	w	16, 18	Barrera et al. (1976)
O. tomentosa	1**, 2, 5, 11	Op	w, m, c	10, 11	Bravo-Hollis (1978)
O. undulata	1**, 11	Op	c	General	Bravo-Hollis (1978); Colunga (1984)
O. velutina	1**, 8, 11	Op	w, m	13, 14, 15, 16	Colunga (1984)
Pachycereus grandis	1**, 2, 4	G col	w	10, 13, 14	Casas et al. (1999a)
P. hollianus	1**, 2, 3, 4, 7	S col	w, m, c	14	"
P. marginatus	1**, 2, 7, 8	S col	w, m, c	10, 14, 16	"
P. pecten-aboriginum	1**, 2, 4, 6, 8, 11	G col	w, m	9, 15, 16	"
P. weberi	1**, 2, 3, 4, 6, 11	G col	w, m	9, 14, 15, 16	"
Peniocereus serpentinus	9	Shr	w, c	14	Arias et al. (1997)
Pereskia grandiflora	8	Shr	c	3	Alcorn (1984)
P. lychnidiflora	7	Shr	w, c	16, 18	Bravo-Hollis (1978); Martínez (1993)
Pereskiopsis aquosa	1**, 5, 8	Shr	w, c	4, 13	Bravo-Hollis (1978)
P. rotundifolia	7, 8	Shr	w, c	13, 14, 15, 16, 18	Arias et al. (1997)
P. velutina	7	Shr	w, c	5	Bravo-Hollis (1978)
Polaskia chende	1**, 2, 4, 7, 11	S col	w, m	14, 16	Casas et al. (1999a)
P. chichipe	1**, 2, 4, 7, 11	S col	w, m, c	14, 16	"
Rhipsalis baccifera	1**, 2, 3, 4, 6	G col	w, m	9, 13, 15, 16	"
Selenicereus donkelaarii	8	Ep	w	17	Martínez (1993)
S. grandiflorus	1**, 2, 3, 4, 5, 7	S col	c	14, 15, 16	Casas et al. (1999a)
S. spinulosus	1**, 2, 3, 4, 6	S col	w, m, c	14, 15, 16	"
Stenocereus beneckei	1*, 2, 7	S col	w	10, 13, 15	"
S. chacalapensis	1**, 2	G col	w	16	"
S. chrysocarpus	1**, 2	G col	w, m	9	"
S. eichlamii	1**	S col	w	18	Bravo-Hollis (1978)
S. fricii	1**, 2, 4, 7	S col	w, m, c	2, 9, 8	Casas et al. (1999a)
S. montanus	1*	S col	w	2, 8	Bravo-Hollis (1978)
S. pruinosus	1*, 2, 7, 11	S col	w, m, c	7, 14, 16	Casas et al. (1999a)
S. queretaroensis	1**, 2, 7	S col	w, m, c	9	"
S. quevedonis	1**, 2, 4, 7	S col	w, m, c	9, 15	"
S. stellatus	1**, 2, 3, 4, 5, 7, 11	S col	w, m, c	13, 14, 15, 16,	"
S. standleyi	1**, 2, 4, 7	S col	w, m, c	9, 15	"
S. treleasei	1**, 2, 4, 7, 11	S col	w, m, c	16	"

Unfortunately, this list includes long-lived cacti that are commonly endangered by this utilization. An alcoholic drink called *colonche* or *nochoctli* may be prepared from fruits of 11 species (Table 9.2). Seeds of 17 species are consumed by people (Table 9.2). In general, seeds obtained from fresh or dried fruits are washed, dried, and roasted to prepare traditional sauces or ground into an edible paste that is consumed with maize tortillas.

Stems and sometimes flowers of 34 species are consumed by humans (Table 9.2). Stems of *Opuntia* spp. and columnar cacti have long been a common food (Callen 1967). At present, consuming young stems of *Opuntia* and *Acanthocereus* as vegetables and utilizing the stems of barrel cacti to prepare candies are locally common, but the young stems of columnar cacti are eaten only during food scarcity. Undoubtedly, cladodes of platyopuntias are by far the most appreciated plants for stem consumption, although many species may be consumed; among the preferred and even commercialized are variants of *O. atropes, O. fuliginosa, O. hyptiacantha, O. jaliscana, O. joconostle, O. megacantha, O. streptacantha, O. tomentosa, O. velutina,* and, of course, *O. ficus-indica* (Colunga 1984). Flower buds are commonly consumed after boiling, e.g., *Pereskiopsis* species, whose leaves are also consumed as greens.

Wood of 9 species of columnar cacti is used in construction of house roofs and fences, and 22 species of *Opuntia, Pereskia, Pereskiopsis,* and columnar cacti, among others, are grown as living fences and/or as barriers for soil protection in terraces of cultivated slopes (Table 9.2). A total of 22 species are utilized as medicine. Among the main diseases traditionally treated with cacti are stomach ache, gastric ulcers, rheumatism, dysentery, diabetes, obesity, and heart diseases (Chapter 13), and some species are used as analgesic, anti-inflammatory, or diuretic agents (Table 9.2).

Also appreciated for their beauty, cacti have been collected, cultivated, and some domesticated as ornamental plants in Mexico and other parts of the world (Chapter 8). For the scope of this chapter, only the 19 species considered as ornamental in rural Mexico are so counted (Table 9.2). The mucilage of *O. ficus-indica* and *Pachycereus hollianus* is utilized as an adhesive (Chapter 13). The dry stems of 25 species are utilized as a fuel for heating and to prepare food, and the stems of *Polaskia chichipe, P. chende,* and *Stenocereus stellatus* are sources of fuel wood for manufacturing pottery.

Peoples of Mexican Mesoamerica gather fruits and other useful products of cacti from wild populations (Table 9.2). In general, they gather fruits selectively, preferring larger fruits of species or variants with juicy pulp, sweeter or, for *xoconoztles,* sourer pulp, or thinner edible pericarp (thicker for *xoconoztles*), shorter and fewer spines, and deciduous areoles (Casas et al. 1997a). Similarly, for collecting edible stems, people take into account the thickness of stems and prefer fewer spines, less mucilage, lack of a bitter flavor, and no fibrous texture (Colunga et al. 1986). When they clear the vegetation for cultivating maize, peasants frequently tolerate or let stand individuals of 19 species of columnar cacti, variants of 13 species of *Opuntia,* and 5 species of other cacti (Table 9.2). They commonly plant vegetative propagules of the spared cacti, enhancing their local abundance. Because these compete with cultivated plants, people carefully select the individuals to spare. Their decisions take into account the usefulness and desirable characteristics of the species and individuals in terms of the products that they produce. About 46 species are cultivated by planting vegetative parts in home gardens or in agricultural plots where they serve as living fences or as barriers to prevent soil erosion (Table 9.2). Vigorous branches or cladodes from wild or cultivated individuals are irrigated, and ash is commonly used as a fertilizer. Individuals cultivated in home gardens may also be derived from seedlings established from seeds dispersed via bird, bat, or human feces. Because people often do not recognize variants of cactus species based on vegetative characteristics, decisions on eliminating or sparing individuals are made when the individuals first produce fruits.

Domestication of Cacti

Columnar Cacti

Although 12 species of columnar cacti are cultivated (Table 9.2), the only cases studied under controlled domestication process are *Stenocereus pruinosus* (Luna 1999), *S. queretaroensis* (Pimienta-Barrios and Nobel 1994), and *S. stellatus* (Casas et al. 1997a, 1999b,c). *Stenocereus pruinosus* occurs in southeast-central Mexico, *S. queretaroensis* in west-central Mexico, and *S. stellatus* is endemic to south-central Mexico (Fig. 9.2). These species occur in the wild in tropical deciduous and thorn-scrub forests, but some wild populations are managed *in situ* and all three species are cultivated (Casas et al. 1999a). They exhibit considerable morphological variation, especially in fruit characteristics, which is presumably partly under genetic control, partly influenced by environmental conditions, and partly the result of human manipulation.

According to archaeological information from caves in Tehuacán, *S. stellatus* has been used for nearly 5,000 years (MacNeish 1967; Smith 1967). Current indigenous groups use and manage this species and *S. pruinosus* mainly for

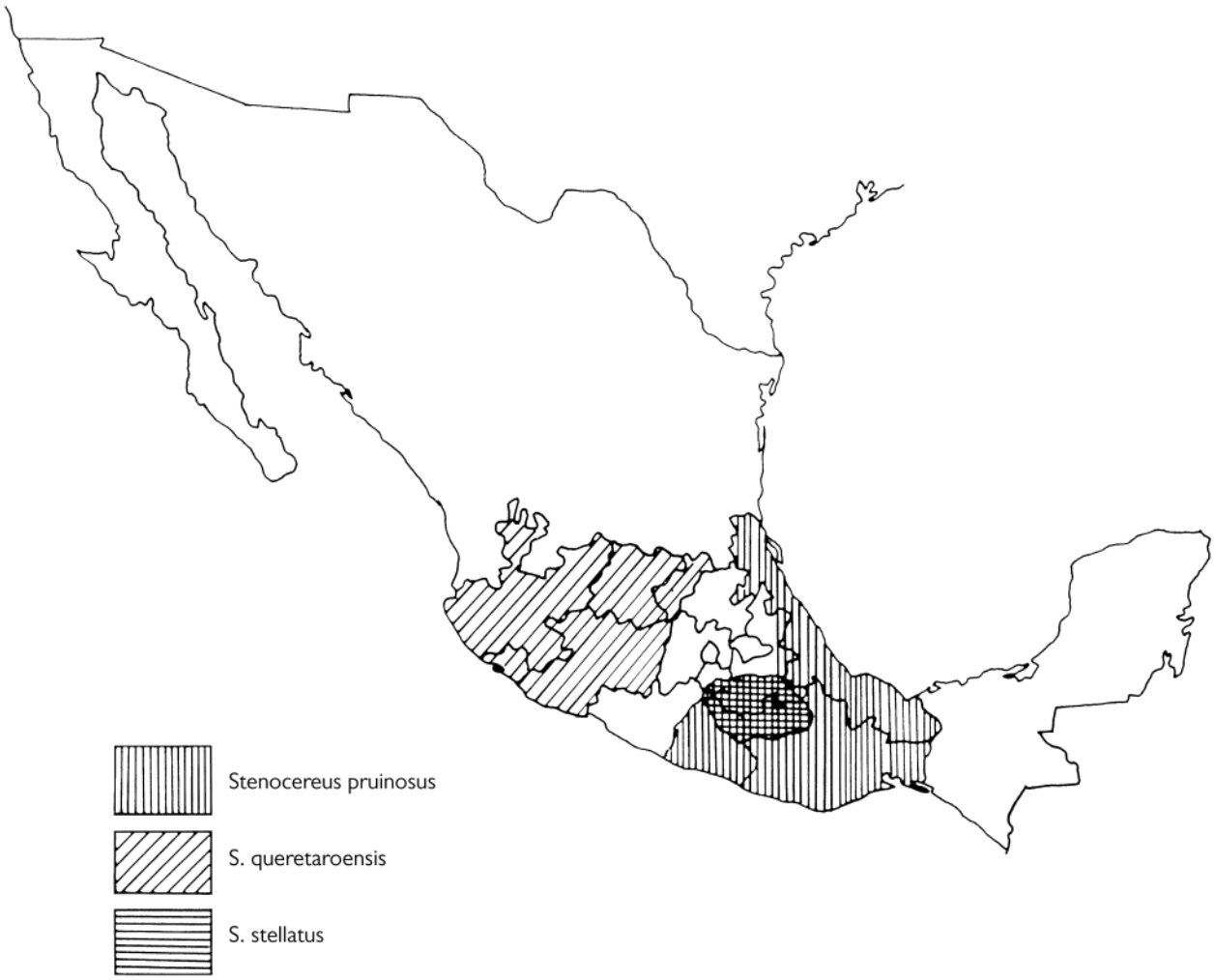


Figure 9.2. Range of *Stenocereus pruinosus, S. queretaroensis,* and *S. stellatus* (Pimienta-Barrios and Nobel 1994; Casas et al. 1997a; Luna 1999).

their edible fruits. Management *in situ* of wild populations of *S. pruinosus* and *S. stellatus* is carried out by keeping desirable phenotypes while removing others, and by cutting and planting branches of desirable phenotypes (Casas et al. 1997a, 1999a). Cultivation is practiced mainly in home gardens, where desirable phenotypes are vegetatively propagated and new variation is incorporated by volunteer seedlings. Similarly, relictual populations of *S. queretaroensis,* associated with pre-Columbian settlements, have been continuously used for long periods in southern Jalisco and Colima (Benz et al. 1997). This species is now widely cultivated in Jalisco and Guanajuato, most of this domestication apparently stemming from the 19th century (Pimienta-Barrios and Nobel 1994).

Pulp color, flavor, amount of edible matter, skin thickness, and spinyness of the mature fruits are the most significant characteristics used in folk classification of variants, assessing quality of products, and selecting individuals of these columnar cacti for propagation (Pimienta-Barrios and Nobel 1994; Casas et al. 1997a, 1999a,b; Luna 1999). Manipulation of these species involves artificial selection. This is particularly intense in home gardens, where manipulation is accomplished by continually planting and replacing individuals, but also is significant in managed populations *in situ,* where selection mainly increases frequencies of favorable phenotypes in wild populations (Casas et al. 1997a).

Where artificial selection has been significant, both management *in situ* and cultivation of *S. stellatus* may change morphology from that in wild populations, especially for those characters that are targets of human selection (Casas et al. 1997a, 1999a). Morphology was therefore compared among individuals from populations under different management regimes. Populations were sampled

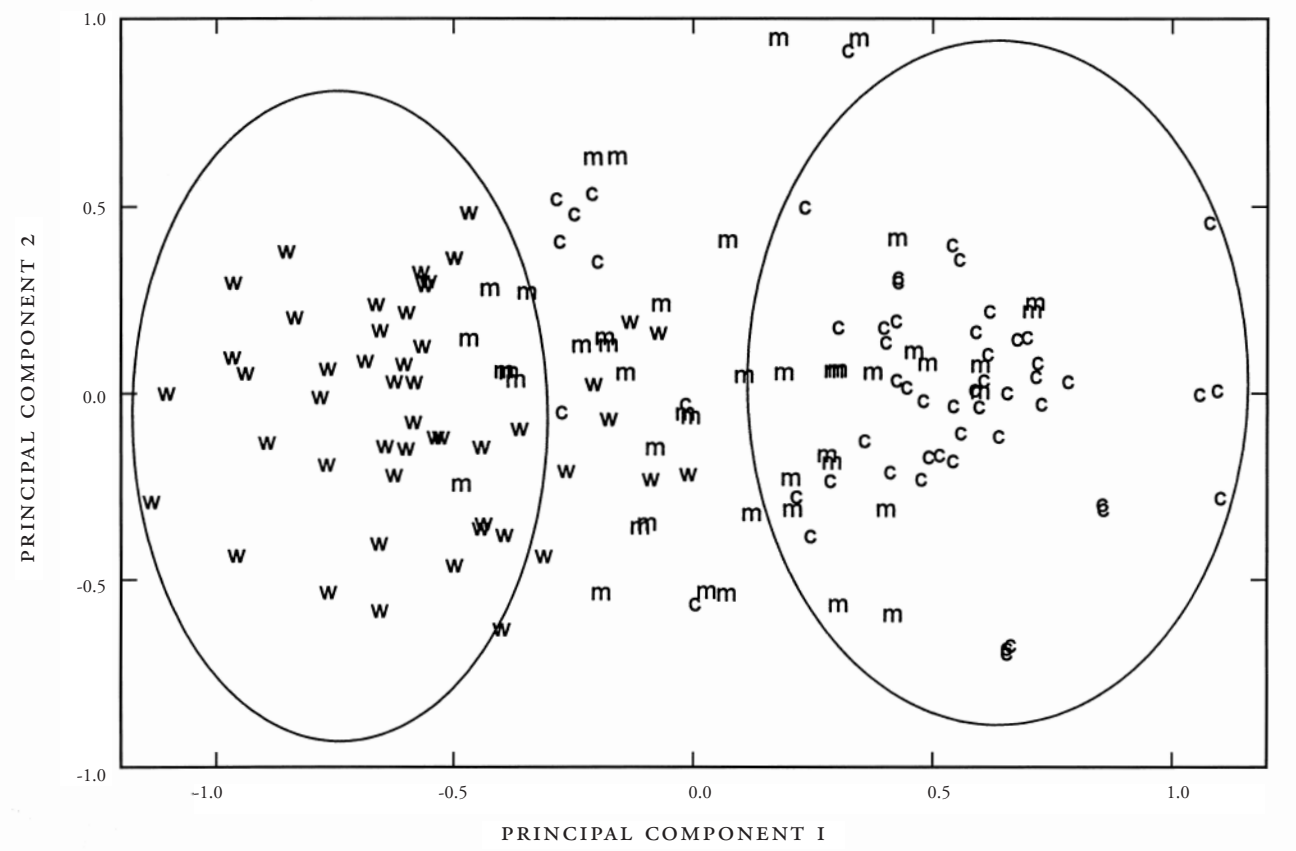


Figure 9.3. Principal component analysis of morphological variation for *Stenocereus stellatus* in the Tehuacán Valley, Puebla (w = wild; m = managed *in situ;* c = cultivated individuals; modified from Casas et al. 1999a). Characters analyzed include numbers and dimensions of fruits (and their parts), seeds, spines, and branches.

from the Tehuacán Valley (Fig. 9.3) and La Mixteca Baja to examine to what extent morphological variation in populations can be related to environmental factors.

Principal component analysis indicates morphological similarities among populations according to their management regime. Most wild individuals in the Tehuacán Valley occupy the left side of the figure, most cultivated ones are on the right side, and those from managed *in situ* populations predominate in the middle (Fig. 9.3). The most significant characters are fruit size, amount of pulp, and seed weight (positive values) and density of spines and skin thickness on fruits (negative values). Cultivated individuals have the largest and least spiny fruits, the thinnest peel, and the heaviest seeds. The number and dimensions of vegetative parts, fruits, and seeds are higher in La Mixteca, whereas the density of spines on the fruits is higher in the Tehuacán Valley. More intensive management leads to larger fruits with a higher proportion of pulp, more and heavier seeds, fewer spines per unit stem area, thinner fruit skin, and a higher proportion of individuals that produce fruits with a green skin and sweet pulp with a color other than red.

Thus, human management has influenced morphological divergence of both managed *in situ* and cultivated populations from wild populations of various species, so domestication may be caused not only by cultivation but also by management of wild populations (Casas et al. 1997a). Although the phenotypes of managed *in situ* and cultivated populations originate from wild populations, some cultivated phenotypes are rare or have not been observed in the wild. This is especially the case for individuals with large fruits and pulp colors other than red. Only 2.3% of the individuals sampled in wild populations have pink or yellow pulp, and other pulp colors (purple, orange, and white) are not observed in the wild (Casas et al. 1999b). On the other hand, 42% of individuals sampled in cultivated populations at La Mixteca have these phenotypes. Success of such phenotypes is low in the wild, and only under human protection (i.e., domestication of *S. stellatus*) are individuals with favorable characteristics

that are scarce or absent in the wild protected and enhanced.

Variation in *S. stellatus* is influenced by environmental conditions, genetic differentiation, and other factors. The clearest environmental difference between the two regions is annual precipitation, higher in La Mixteca (average of 740 mm) than in the Tehuacán Valley (510 mm). In all populations, anthesis of *S. stellatus* is predominantly nocturnal, and bats are the most probable pollinators (Casas et al. 1999c). With bats as pollinators, movement of pollen between populations is expected, as bats can commute 30 km from their roosts (Sahley et al. 1993). Isolation by distance within regions is therefore unlikely between wild, managed *in situ,* and cultivated populations, because distances separating these populations are generally less than 10 km. In addition, flowering in wild and cultivated populations overlap by at least 75 days, indicating that temporal barriers for pollination between populations are also unlikely.

Stenocereus stellatus is out-crossing, and major differences exist between wild and cultivated populations. However, experimental crosses indicate pollen incompatibility between certain cultivated phenotypes, especially those with the greatest domestication. This can partly explain the morphological and genetic divergence among wild, managed, and cultivated populations. Nevertheless, the absence in wild populations of the phenotypes typical of home gardens may also be explained by failures in seed germination or in the establishment of these variants under wild conditions. Similar to results with *S. stellatus,* Luna (1999) analyzed the morphology of wild, managed *in situ,* and cultivated trees of *S. pruinosus,* finding significant differences in fruit mean weight: wild, 38 g; managed *in situ,* 70 g; and cultivated, 188 g. Seeds are larger and more numerous in cultivated variants. For *S. queretaroensis,* weights of fruit from wild trees (60–90 g) are higher than those from cultivated trees (over 130 g; Pimienta-Barrios and Nobel 1994). For *S. fricii* in Michoacán, fruit weight in wild populations is extremely variable but averages 130 g, whereas fruits of the cultivated variants average 230 g (Rebollar et al. 1997).

Opuntia *Species*

Opuntia ficus-indica, O. megacantha, O. streptacantha, O. robusta var. *larreyi,* and *O. joconostle* are the most commonly cultivated opuntias (Bravo-Hollis 1978). Yet in the El Bajío region of Guanajuato, Mexico, 16 *Opuntia* species are used for their edible products: young cladodes (nopalitos) and fruits (Colunga et al. 1986). The edible products of *Opuntia* are very important in the local peasant economy, because they are particularly abundant before the harvest season of maize and sometimes the latter is scarce; their commercialization determines about 20% of the annual income of local people (Colunga 1984). Interactions include gathering, tolerance, and enhancement *in situ* in areas cleared for agriculture, and cultivation in agricultural plots and home gardens.

The different utilization and management of *Opuntia* species and particular populations is due to the recognition of specific attributes and morphological differences among species and variants (Colunga 1984). Local people recognize nearly 70 variants belonging to the 16 species, which are broadly classified as 'manso' (docile) and 'de monte' (from the mountains). The 'manso' variants include plants whose edible products are of better quality but are dependent on humans for survival. These presumably domesticated variants include 17 of *Opuntia crassa, O. ficus-indica, O. megacantha, O. robusta* var. *larreyi,* and *O. undulata.* The 'de monte' variants do not depend on humans for survival and are presumably wild or weedy variants. Within the 'de monte' variants are plants producing fruits with thick sour edible peel named *xoconoztles* (including variants of *Opuntia joconostle* and two variants of *O. lasciacantha*), others producing fruits with thin peel and sour pulp called *jocotunas* that are consumed entire as greens (including variants of *Opuntia* aff. *leucotricha* and one variant of *O. streptacantha*), and others producing fruits with thin peel and sweet pulp called *tunas.* Among the characteristics for classifying and selecting phenotypes for differential management of *Opuntia* variants are fruit flavor, color, peel thickness and hardness, form, size, and spinyness as well as cladode size.

Colunga (1984) performed multivariate statistical analyses with 9 individuals of each of 70 variants of 16 species and considered 69 morphological characters to explore patterns of morphological similarity among the variants. These analyses consistently separated the 'manso' and the 'de monte' variants. Nearly 34 'de monte' variants of the species *O. atropes, O. fuliginosa, O. hyptiacantha, O. jaliscana, O. joconostle, O. lasiacantha, O. megacantha, O. streptacantha, O. tomentosa,* and *O. velutina* are managed *in situ* and are morphologically intermediate between the 'manso' and the 'de monte' variants. Thus, artificial selection apparently causes a morphological divergence not only between the wild and domesticated variants, but also between the wild and the managed *in situ* variants. The characters with higher significance in defining these groups relate to the dimensions of fruits and cladodes, the frequency of areoles on fruits and cladodes, fruit and seed form, and seed number and weight (Colunga et al. 1986). Of the species studied by Colunga (1984), *O. megacantha*

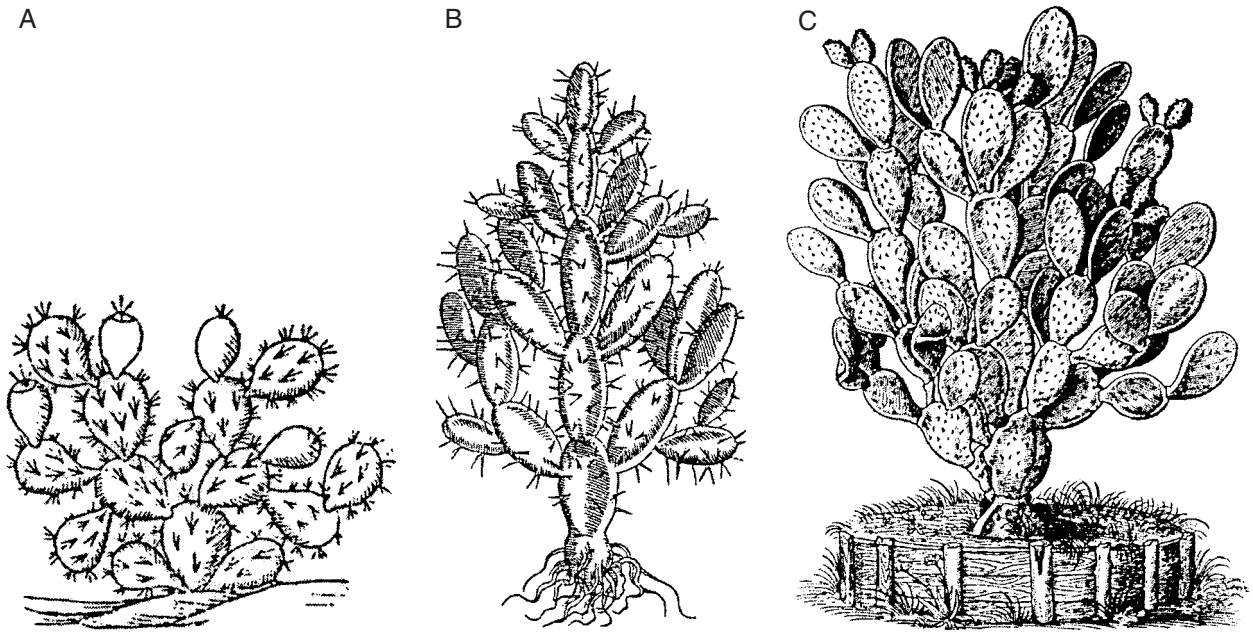


Figure 9.4. Various early depictions of opuntias: (A) the first opuntia depicted by a European illustrator (Oviedo y Valdés 1535); (B) drawing of an opuntia in Mattioli's 1558 edition of *De Materia Medica*; and (C) drawing of an opuntia in Mattioli's 1568 edition of *De Materia Medica*.

is the only taxon having wild, managed *in situ,* and domesticated/cultivated variants; based upon morphological data, the three types clearly form discrete groups according to their management (Colunga et al. 1986), as for *S. stellatus* (Fig. 9.3). Fruit, cladode, and seed dimensions are the most significant characters for this classification, and the management regime thus apparently plays a role in domestication of cacti.

Diffusion of Cacti to Other Regions of the World

Hundreds of species of cacti are presently part of plant collections in botanical gardens and some have become popular as ornamental plants worldwide. The "dragon fruit" *Hylocereus undatus* is an important crop in southeastern Asia after its introduction to the Philippines by Spaniards in the 16th century; trials are being conducted in Israel and the United States for cultivating it along with some of the fruit-producing columnar cacti (Chapter 11). But, undoubtedly, platyopuntias are the cacti most widespread out of their original range (Chapter 10), their dissemination having been initiated by humans after the conquest of the New World by Europeans. The first European to report on American platyopuntias was the Spanish state officer Oviedo y Valdés (1526), who wrote about two prickly pear cacti common on the island Hispaniola (now Haiti). In a later work (Oviedo y Valdés 1535), these plants were described in greater detail, one of them being depicted for the first time in the drawing of a European illustrator (Fig. 9.4A).

The wonder of the plants of the New World ("so beautiful and so different from ours," as Columbus wrote on his first pages about America) turned into bewilderment over the strangeness. The flora of the Old World did not include plants that were morphologically similar to platyopuntias, therefore Oviedo y Valdéz could not tell whether "this is a tree or rather a monster amidst trees," and he wrote that great painters, such as Leonardo da Vinci and Andrea Mantegna, would be necessary to describe it properly. His incredulity was shared by other European travelers, who in the subsequent 50 years talked about the plant, struck by some of its amazing features: leaves growing one upon the other into such a tree that it was impossible to find something "wilder or uglier" in the plant kingdom (Oviedo y Valdés 1526) and fruits that turned the urine red, which aroused great fear and became a prank played on newcomers. The fruits, called *tunas* by Oviedo y Valdés (1535), were commonly sold in markets; they were so delicious that his fellows "knew and ate [them] . . . with pleasure" and they were "as lovely as figs." The name given to the best-known species, *Opuntia ficus-indica,* reflects this supposed morphological resemblance and the geographical origin (the West Indies). The fruits of other opuntias mentioned by Oviedo y Valdés were mashed, dried, and used as dyestuff, while their cladodes were used in compresses to treat bone fractures, probably because of the anti-inflammatory action of mucilage (the "bone-fixing tree").

Colonial Period

When the Spanish conquistadors landed in Mexico, Oviedo y Valdés's curiosity was renewed and enhanced by the symbolic role that opuntias played in the complex Aztec cultural world. However, the interest in the commercial exploitation of the plant and especially in its fruits (offered as a present to the invaders in 1519 during Hernando Cortés's march on the Aztec capital [Diaz del Castillo 1991])did not go beyond a vague and cautious consideration, similar to that shown for many of the foods eaten by the American natives. Although Europeans liked its fruits as much or more than the local populations (Toribio de Motolinía 1541 and López de Gomara 1552, cited in Donkin 1977), the prickly pear was not introduced to Europe for food but as an ornamental plant. This was also the case for most American species that only later became staple crops and foods throughout Europe. One of the tasks of European travelers was to collect new and curious-looking plants, and prickly pears undoubtedly fell into that category.

Despite the lack of records, prickly pears are thought to have been first introduced to Europe in western Andalucía, probably in Seville. Beginning in 1495, this city had become the center of trade with the Americas through its *Casa de Contratación;* its numerous garden plants were acclimatized and studied for their medicinal properties (Valdes et al. 1992). Because of its importance to the Mesoamerican civilization, the first plant to be brought to Spain was probably *Opuntia ficus-indica.* This species, which was likely the one described by López de Gomara in 1552 (taking for granted that it was already known in Spain), seems to be represented in the first illustration of a specimen grown in Europe, published in the 1558 edition of *De Materia Medica* by the Italian physician Mattioli (Fig. 9.4B). A product of the plant, indirectly obtained by the insect that feeds on the plant, was apparently known and appreciated by the Spaniards more than the plant itself—the red dye, called *grana cochinilla* (cochineal). The conquistadors were impressed by the wonderful colors of Aztec artifacts, and probably as early as 1520—although the first record dates back only to 1543—small quantities of the dyestuff were brought to Spain. The new product met with instant success in European markets, because its dyeing power was ten times greater than kermes, the coloring matter used in the Old World and previously considered the best of red dyes. In the last quarter of the 16th century, Spain annually imported 70,000 to 90,000 kg of *grana cochinilla,* and this substance became one of the the most sought-after commodities from the American continent, preceded only by precious metals (Donkin 1977).

Spread of Platyopuntias in Europe

In the second half of the 16th century, prickly pears began to spread rapidly, first in many botanical gardens all over Europe. In the meantime, more knowledge about the plant arrived from America: Francisco Hernández from 1571 to 1576 and Sahagún in 1570 described several varieties, Cervantes de Salazar in 1554 pointed out that cladodes could easily take root, and G. Gómez de Cervantes in 1599 provided the first hints on growing techniques (Donkin 1977; Alvarez López 1946). Among European countries, Italy was particularly attracted to the new American plant—it was the Renaissance, arts and sciences were flourishing, and a deep interest in plants coming from the New World developed. Nonetheless, the prickly pear was always looked upon with suspicion. Galeotto Cei (1991) considered it so "malignant" that "however appreciated it may be in Italy, I would not wish to see or find it anywhere." A physician from Siena, Pier Andrea Mattioli, had a different attitude: he regarded the plant as "one of the wonders of nature," and his interest grew constantly in the various editions of his famous book (Mattioli 1558, 1568). No mention of prickly pears is made in the first issue of 1544 (Donkin 1977), whereas in 1558 the plant is depicted by a drawing, and two more illustrations are present in the 1568 version (Fig. 9.4C). The curious appearance of the plant, which in 1580 Soderini associated with the turkey to show the peculiarity of American nature (Tangiorgi Tomasi et al. 1990), helped it spread from botanical gardens to aristocratic estates all over Europe. In Italy, prickly pears were grown in Florence (Mattioli 1568). Dodonaeus in 1583 reported their dissemination into Germany and Holland and Gerard in 1596 into England (Alvarez López 1946).

More evidence of this popularity is provided by botanical drawings and engravings representing the plant, and by its appearance in the figurative arts. Platyopuntias are depicted in a painting by Bruegel the Elder ("Land of Plenty," 1567) as well as in some of the most beautiful botanical illustrations of the Renaissance, such as the watercolor of *Iconographia Plantarum* by Ulisse Aldovrandi (end of the 16th century; Baldini 1990) and the tables of *Hortus Eystehensis* (1600). The plant was highly rated and is considered necessary in a royal garden (Agostino del Riccio [undated but end of the 16th century], cited in Tangiorgi Tomasi et al. 1990), or thought to have occurred in Eden, as one of Switzer's 17th century xylographies shows.

History of Name

In the 17th century, prickly pears were "grown in the roof gardens of noblemen's mansions" (Bahuin 1650–1651, cited

in Alvarez López 1946). Being closely linked to the botanical tradition of ancient Greece, Mattioli (1568) deemed impossible the acceptance of a new species and traced the newly discovered plants back to the flora of the classical world. In *Commentarii in sex Libros Pedacii Dioscoridis,* the prickly pear is mentioned in a chapter about the Mediterranean fig (*Ficus carica*). Two Indian figs are described: a large tree with branches that root, identified with the same plant mentioned by classical writers such as Theophrastus, Strabo, and Pliny; and another Indian fig, introduced from the West Indies "in our time," the fruits of which are called *tune* (tuna) by Indians. Mattioli believed the latter to be *Opuntia plinii,* the plant already described by the great Latin agronomist and named after Opunte, a town in Locrid (Greece), where grew a plant the leaves of which could root.

The fact that an American plant could be known to Greeks and Romans did not seem absurd to Mattioli and to many other European botanists after him. Some did raise doubts, such as the Spaniard Laguna in 1563, who "dared not affirm" that the prickly pear was Pliny's plant. Others did not seem to see the contradiction: in fact, Fragoso in 1572 and Rouvillium in 1587 believed it to be an American plant, but claimed it was already known by the ancients (Alvarez López 1946). Although Parkinson in 1619 stated with certainty that this could not be the plant described by Pliny, others persisted in believing the fallacy for a long time, essentially based on the observation that cladodes take root (Alvarez López 1946). The occurrence of the prickly pear in natural and cultural landscapes of Mediterranean Europe is so common, popular texts still say that this plant is a native species, or that it was introduced from the East Indies by the Arabs, as Gerard claimed in 1633. Considering that the various botanical names contain a semantic error, either based on the appearance of the fruits or on the geographical origin (*Cactus ficus-indica* Linnaeus, 1753; *Opuntia ficus-indica* [L.] Miller, 1768; *Cactus opuntiae,* Gussone, 1827–8; *Opuntia ficus-barbarica* Berger, 1912), one can perfectly agree with de Candolle (1883) when he said that "everything about this name is false and ridiculous!"

Naturalization in Europe

In northern Europe, platyopuntias cannot survive winter outside the privileged space of botanical gardens. In milder Mediterranean areas, the plants have found optimal environmental conditions, spreading and naturalizing so as to become one of the typical features of Mediterranean landscapes (Barbera et al. 1992). Prickly pear cacti can grow in places where the average minimal temperature does not go below 1 to 2°C, and average relative humidity does not remain lower than 40% for more than 1 month. In regions where the plants are common and commercially exploited, annual rainfall ranges from 400 to 600 mm, but they can also grow in areas with only 200 mm or up to 800 mm annually (in the latter case, the lithologic substrate must favor soil drainage). Under these conditions, platyopuntias grow independently of the lithologic matrix, even if they are typically found on volcanic soils and calcareous rocks, where they occur in scrub patches together with *Euphorbia dendroides, Artemisia arborescens, Calycotome infesta,* and other species (La Mantia et al. 2001). According to Le Houerou (1996), the major occurrence of platyopuntias in the western Mediterranean is due to a shorter and less severe dry season, which favors the natural spread of the species, in comparison with drier eastern regions. In addition to *O. ficus-indica,* other naturalized species growing on Mediterrean coasts are *O. decumana, O. dillenii, O. stricta, O. vulgaris, O. amyclaea,* and *O. robusta,* the last two of which inhabit frost-free areas only.

Dissemination of species was clearly encouraged by their widespread use in Mediterranean farming. After southern Spain, the first regions that knew and valued prickly pear were North Africa and Sicily, because of geographic contiguity or social and political relationships with the Spanish peninsula. Soon platyopuntias spread all over the Mediterranean coast and, taken aboard ship to prevent scurvy, followed European colonization and reached the remaining parts of Africa, Asia, and Australasia. In the Mediterranean, prickly pears turned out to be an inexhaustible source of products, first as a subsistence crop and later as a cash crop. The local populations immediately appreciated the new species, but neither cochineal production nor human consumption of young cladodes (nopalitos; both common in Mesoamerica) gained ground. Some attempts at cochineal culture were made, but only in the 19th century in Malta (1828), Algeria (1834), and Sicily (1860). The Spaniards, who held the monopoly of the cochineal industry, banned the export of insects until 1777, when the botanist N. J. Thierry de Menonville managed to introduce them to French dominions. Attempts at raising cochineal insects feeding on *O. ficus-indica* or *Nopalea cochenillifera* failed in the Mediterranean area, because these coccids cannot bear the combination of excessively low temperatures and frequent winter rainfall. The cochineal industry proved successful only in the Canary Islands, where it became a profitable economic activity, especially on the island of Lanzarote, and remains so since its introduction in 1826 to 1835 (Donkin 1977; Baranyovits 1978). On the other hand, the use of nopalitos for food has

remained almost unknown in Europe; the only food habit that bears some resemblance to its use in Mesoamerica is found in some areas of inner Sicily, where the fruit skin is breaded and fried.

Platyopuntias in Sicily

In Sicily, *O. ficus-indica* became very popular and acquired considerable economic significance for its fruits. They became an important staple crop, but were also considered as a forage crop in extensively farmed inner regions. Platyopuntias were grown to ensure forage in times of emergency and were planted near rural buildings and animal shelters to form enclosures or dense scrub. They originally occurred as fruit plants in "pleasant gardens," as Bonanno reported in the 17th century, but their cultivation soon spread (Coppoler 1827), both in inner areas and on the coast, where they were to be found in "dry" orchards together with vines and olive, almond, carob, and pistachio trees. The fruit soon entered local markets: a platyopuntia is depicted on what seems to be a market stall in a still life by an unknown Sicilian painter who lived around 1640 and was named "maestro del ficodindia" (master of the prickly pear) because of this work (Barbera and Inglese 1993).

Platyopuntias had a leading role in the food habits of Sicilians. They were described as "the bread of the poor," and De Gasparin, a French agronomist who visited the island around 1840, said they were "the manna, the blessing of Sicily, the equivalent of the banana tree to equinoctial countries or the breadfruit tree to the Pacific Islands" (Biuso Varvaro 1895). The fruits can be eaten fresh, or are sun-dried and stored for the winter, following a peasant tradition. The juice, concentrated through boiling and seasoned with flour and spices, is used in recipes for special cakes called 'mostaccioli,' or for chutneys. The fruits were also used for ethanol production; in 1865 a plant in Catania obtained 2,500 liters per day and around 1940, in search of energy sources to ensure economic self-sufficiency to the country, this opportunity was again considered, and platyopuntias were extolled. Among other Sicilian rural traditions linked to this cactus are the production of a red dye obtained from the fruits of *O. dillenii* and the use of a decoction of dried flowers for diuretic purposes, a natural remedy that is still widely used and justified by the presence of a glucosidic flavonoid (isoramnethin) and a high potassium content. In Spain, the flowers were used to treat seizures in children in the 18th century. Convex cladodes served as plates in picnics, or as containers for the manna extruding from the tapped trunk of *Fraxinus angustifolia.* Sicilian farmers also use prickly pears for soil conservation, as mulch, and as windbreak hedges (Barbera 1994).

Fresh fruit production became the most important commercial exploitation, particularly beginning in the 19th century. In coastal areas, especially near the main towns, production flourished for local and export markets (Genoa, Marseille, London, and, from the 1850s, New York). Commercial success was favored by a cultivation technique called *scozzolatura,* whereby in autumn fruits of better quality and preservability than summer produce were obtained and put on the market when competition was less. The origins of this technique reflect the culture of the archaic Sicilian rural world. The agronomic chronicle by Alfonso Spagna (1884) gives an account of a quarrel breaking out, in a town not far from Palermo, between a farmer, who did not want to sell his product, and a merchant, who took his revenge by knocking down the fruits in full bloom. In Ventimiglia Sicula (famous for its delicious fruits that were sold in Palermo), a dispute arose between a son, who in May 1819 performed thinning to have bigger fruits, and a father who, ignoring the beneficial effect of this technique, removed all the fruits from the plant. In both cases and against all expectations, the plants blossomed again, and the late-ripening fruits were of higher quality.

Expansion to Other Mediterranean Regions

In Sicily, spineless forms were widely used for forage in the 1920s, when they were replaced—albeit keeping a minor role—by other crops that were thought to be more suitable for the climatic conditions of the region. From 1920 to 1930, the plant enjoyed great success in drier North African areas, being widely grown both in specialized farms as a forage crop and in extensive areas for erosion control, land reclamation, and rehabilitation. Platyopuntias were so important that Monjauze and Le Houerou (1965) regarded their dissemination as the "pre-arboricultural stage of farming," and described them as the plants that made possible the shift from nomadism to agriculture. Today in North Africa, especially in southern Tunisia, the vigorous action taken by programs against desertification, soil erosion, and dune movement, combined with the production of fodder for livestock, envisages the use of platyopuntias together with *Acacia* and *Atriplex* species (Chapter 12). To encourage forage production, much research was carried out in Tunisia and Algeria on cold-hardy species and clones of *O. ficus-indica,* many of which were brought from Mexico to be grown in arid highlands (Le Houérou 1996).

Platyopuntias are now common in arid regions that are subject to water and wind erosion. They prove effective in preventing soil loss, accumulating wind borne deposits, and reducing land degradation. They are also used to slow

and direct sand movement, enhance the restoration of vegetative cover, stabilize the soil, and prevent water from destroying land terraces built to reduce runoff. The popularity of platyopuntias in North Africa is demonstrated by extensive cultivation areas begun in the 1950s, ranging from 700,000 to 1,000,000 hectares in Tunisia, Algeria, and Morocco (Nefzaoui and Ben Salem 2000).

Platyopuntias currently play a minor role in other Mediterranean countries. In Spain, Greece, and Turkey, they frequently occur in home orchards or vegetable gardens for human and animal consumption (fruits are particularly appreciated by pigs), but it is not common for commercial exploitation. They are also popular in Israel, where in the Negev Desert specialized farms covering hundreds of hectares can obtain two crops per year. The fruit of platyopuntias is called *sabra* in Israel, the same term used for people native to the country (because their character is like the fruit, spiny outside but sweet inside). Further indicating the exotic origin of the species are other popular names: e.g., the Arabs call it "Christian fig" and the French "Barbary fig" (from the ancient name of North Africa).

Conclusions and Future Prospects

Although a broad spectrum of cacti could have been crucial for sustenance of Mesoamerican people for a long time, only a few species have been recorded in archaeological excavations, and uncertainty exists about forms of utilization and management. The conjunction of archaeological and botanical research may clarify these aspects. In particular, Mesoamerican people currently utilize and manage many species of cacti. People presently decide how to manipulate cacti according to the quality of their products and their roles in human subsistence. The species and varieties cultivated or managed *in situ* are generally those with the most useful fruit characteristics. As found for *Stenocereus stellatus* (Casas et al. 1997a), cultivation is particularly intensive where the commercialization of fruits or their consumption by households leads to more and/or better fruits. Availability of plant resources is another crucial factor influencing their management; e.g., *S. stellatus* is intensively cultivated in places where wild populations are scarce, but not where they are abundant. Although species such as *Mitrocereus fulviceps, Neobuxbaumia tetetzo, N. mezcalaensis,* and *Pachycereus weberi* produce good quality fruits, and species of barrel cacti produce economically important stems (Table 9.2), they are not cultivated *ex situ,* because their slow growth makes the effort of sowing seeds and taking care of seedlings unrewarding for decades. Slow growth may not be relevant for decisions on managing wild populations of such species *in situ.* However, artificial selection favoring particular phenotypes *in situ* may reflect difficulties in increasing the frequency of desirable phenotypes by intentional direct propagation. Furthermore, when the seeds of desirable phenotypes are sown, the additive genetic variance of desirable traits can make it uncertain that the phenotypes selected are those expressed in the progeny. In contrast, the fixation of desirable characters in species with vegetative propagation, such as *S. pruinosus, S. queretaroensis,* or *S. stellatus* and *Opuntia* species, is relatively easy.

Artificial selection is carried out by identifying and subsequently increasing by vegetative propagation individuals that have desired phenotypes from wild, managed *in situ,* or cultivated populations. Artificial selection is also applied when plants of desired forms are preferentially spared or protected when land is cleared, or when seedlings are spared in cultivated populations until their fruits can be evaluated. Artificial selection has achieved significant results for species such as *Stenocereus fricii, S. griseus, S. pruinosus, S. queretaroensis,* and *S. stellatus* (Pimienta-Barrios and Nobel 1994; Casas et al. 1997a, 1999a, b; Rebollar et al. 1997), as well as for *Opuntia crassa, O. ficus-indica, O. megacantha, O. robusta* var. *larreyi, O. undulata,* and probably *O. joconostle* (Colunga 1984; Bravo-Hollis 1978). Artificial selection can also be significant for *Escontria chiotilla, Myrtillocactus geometrizans, M. schenckii, Pachycereus hollianus, P. marginatus, Polaskia chichipe,* and *P. chende* (Casas et al. 1999a) and variants of *Opuntia atropes, O. fuliginosa, O. hyptiacantha, O. jaliscana, O. joconostle, O. lasiacantha, O. megacantha, O. tomentosa, O. streptacantha,* and *O. velutina* (Colunga, 1984), which are intensely cultivated and/or managed *in situ* and which exhibit morphological variation in characters that are targets of human preference. The developing case studies of *Opuntia* and *Stenocereus* species provide a model of *in situ* and *ex situ* artificial selection that can help analyze patterns of domestication and can lead to hypotheses for testing in future research.

Ornamental cacti, *Hylocereus undatus,* columnar cacti, and *Opuntia* species are the main groups of the family Cactaceae diffused by humans in a process lasting about 500 years. Apart from *Opuntia,* particular forms of utilization and selection of these cacti should be documented in their new environments and under new human cultural conditions. The consequences of artificial selection in the evolution of these species needs to be evaluated. Particularly interesting will be a comparison in morphological and genetic changes developed during these 500 years in the context of human cultures and environments of the New and Old Worlds.

In any case, platyopuntias have become an integral part of the Mediterranean landscape and agricultural economy. To further develop its cultivation requires higher-quality and glochid-free fruits. Today, consumption is mostly confined to immigrants of rural origin, who are already familiar with the fruit in their homelands. In countries such as Belgium, France, Germany, and Great Britain, demand comes mainly from migrant workers from Italy and Africa. The market would expand considerably by attracting a different category of consumers—people curious about unusual and exotic products. The extension of the marketing period and the integration with produce from the southern hemisphere would increase consumption in the Mediterranean countries and ensure constant presence on the market. As for its use as a forage crop, the cloning of cold-hardy and salt-resistant varieties, or varieties with a higher protein content, as well as the introduction of this species in balanced diets, can increase consumption in arid and semiarid regions. The role played by platyopuntias in the economy and the environment, considering also the scenario of global climatic change and increasing desertification, should become increasingly important (Barbera 1995).

Acknowledgment

We thank Javier Caballero and Laura Cortés, who facilitated consulting with the Banco de Información Etnobotánica de Plantas Mexicanas (BADEPLAM) of the Jardín Botánico, Instituto de Biología, UNAM.

Literature Cited

Acuña, R., ed. 1985. *Relaciones Geográficas del Siglo XVI: Tlaxcala,* Vol. II. Universidad Nacional Autónoma de México, Mexico City.

Alcorn, J. 1984. *Huastec Mayan Ethnobotany.* University of Texas Press, Austin.

Alfonso Spagna, F. 1884. *La Coltivazione Forzata del Fico d'India a Palermo.* Stabilimento Tipografico Virzù, Palermo.

Alvarez López, E. 1946. Las plantas de America en la botanica Europea del siglo XVI. *Revista de las Indias* 5: 218–288.

Arias, S., S. Gama, and U. Guzmán. 1997. *Flora del Valle de Tehuacán-Cuicatlán. Fascículo 14 Cactaceae.* Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City.

Baldini, E. 1990. Fruits and fruit trees in Aldrovandi's "Iconographia plantarum." *Advances in Horticultural Science* 1: 61–73.

Baranyovits, F. L. C. 1978. Cochineal carmine: An ancient dye with a modern role. *Endeavour, New Series,* 2: 85–92.

Barbera, G. 1994. *Il Ruolo del Ficodindia nell' Agricoltura delle Regioni Aride e Semi-aride.* Atti dell'Accademia di Scienze, Lettere ed Arti, Palermo.

Barbera, G. 1995. History, economic and agro-ecological importance. In *Agro-ecology, Cultivation and Uses of Cactis Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 1–19.

Barbera, G., F. Carimi, and P. Inglese. 1992. Past and present role of the Indian-fig prickly pear *(Opuntia ficus-indica* [L.] Miller, Cactaceae) in the agriculture of Sicily. *Economic Botany* 46: 10–20.

Barbera G., and P. Inglese. 1993. *La Coltura del Ficodindia.* Edagricole, Bologna.

Barrera, A., A. V. Barrera, and R. M. López Franco. 1976. *Nomenclatura Etnobotánica Maya. Una Interpretación Taxonómica.* Instituto Nacional de Antropología e Historia, Mexico City.

Benz, B. F., F. Santana M., J. Cevallos E., E. Muñoz M., J. Rosales A., and M. Rosales A. 1997. The structure and productivity of relict stands of pitaya (*Stenocereus queretaroensis;* Cactaceae), Jalisco, Mexico. *Economic Botany* 51: 134–143.

Berlin, B., D. E. Breedlove, and P. H. Raven. 1973. *Principles of Tzeltal Plant Classification.* Academic Press, New York.

Biuso Varvaro, S. 1895. *Il Ficodindia.* Marsala Editore, Palermo.

Bravo-Hollis, H. 1978. *Las Cactáceas de México,* Vol. I. Universidad Nacional Autónoma de México, Mexico City.

Bravo-Hollis, H., and H. Sánchez-Mejorada. 1991. *Las Cactáceas de México.* Vols. II and III. Universidad Nacional Autónoma de México, Mexico City.

Bye, R. A. 1993. The role of humans in the diversification of plants in Mexico. In *Biological Diveristy of Mexico* (T. P. Ramamoorty, R. Bye, A. Lot, and J. Fa, eds.). Oxford University Press, New York. Pp. 707–731.

Caballero, J. 1992. The Maya homegardens of the Yucatán peninsula: Past, present and future. *Ethnoecologica* 1: 35–54.

Callen, E. O. 1967. Analysis of the Tehuacán coprolites. In *Prehistory of the Tehuacan Valley. Vol. 1. Environment and Subsistence* (D. S. Byers, ed.). University of Texas Press, Austin. Pp. 261–289.

Candolle, A. de (1883). *L'origine delle Piante Coltivate.* Fratelli Dumolard Editore, Milan.

Casas, A., M. C. Vázquez, J. L. Viveros, and J. Caballero. 1996. Plant management among the Nahua and the Mixtec from the Balsas River Basin: An ethnobotanical approach to the study of plant domestication. *Human Ecology* 24: 455–478.

Casas, A., B. Pickersgill, J. Caballero, and A. Valiente-Banuet. 1997a. Ethnobotany and the process of domestication of the xoconochtli *Stenocereus stellatus* (Cactaceae) in the Tehuacán Valley and La Mixteca Baja, Mexico. *Economic Botany* 51: 279–292.

Casas, A., J. Caballero, C. Mapes, and S. Zárate. 1997b. Manejo de la vegetación, domesticación de plantas y origen de la agricultura en Mesoamérica. *Boletín de la Sociedad Botánica de México* 61: 31–47.

Casas, A., J. Caballero, and A. Valiente-Banuet. 1999a. Use, management and domestication of columnar cacti in south-central Mexico: A historical perspective. *Journal of Ethnobiology* 19: 71–95.

Casas, A., J. Caballero, A. Valiente-Banuet, J. A. Soriano, and P. Dávila. 1999b. Morphological variation and the process of domestication of *Stenocereus stellatus* (Cactaceae) in central Mexico. *American Journal of Botany* 86: 522–533.

Casas, A., A. Valiente-Banuet, A. Rojas-Martínez, and P. Dávila. 1999c. Reproductive biology and the process of domestication of *Stenocereus stellatus* (Cactaceae) in central Mexico. *American Journal of Botany* 86: 534–542.

Casas, A., A. Valiente-Banuet, J. L. Viveros, J. Caballero, L. Cortés, P. Dávila, R. Lira, and I. Rodríguez. 2001. Plant resources of the Tehuacán-Cuicatlán Valley, Mexico. *Economic Botany* 55: 129–166.

Cei, G. 1991. Viaggio e relazione delle Indie, 1539–1553. In *Nuovo Mondo, gli Italiani, 1492–1565* (P. Collo and P. L. Crovetto, eds.). Giulio Einaudi Editore, Torino, Italy.

Colunga, P. 1984. Variación morfológica, manejo agrícola y grados de domesticación de *Opuntia* spp. en El Bajío Guanajuatense. Master's Thesis, Colegio de Postgraduados, Chapingo, Mexico.

Colunga, P., E. Hernández-Xolocotzi, and A. Castillo. 1986. Variación morfológica, manejo agrícola tradicional y grado de domesticación de *Opuntia* spp. en El Bajío Guanajuatense. *Agrociencia* 65: 7–44.

Coppoler, S. 1827. Saggio sul ficodindia, sua coltivazione e modo di ottenerne i frutti tardivi. *Giornale di Scienze, Lettere ed Arti per la Sicilia* 57: 3–50.

Darwin, C. 1868. *The Variation of Plants and Animals under Domestication.* John Murray, London.

De la Cruz, M., and J. Badiano. 1964. *Libellus de Medicinalibus Indorum Herbis. Codex Barberini.* Instituto Mexicano del Seguro Social, Mexico City.

Del Castillo, R., and S. Trujillo. 1991 Ethnobotany of *Ferocactus histrix* and *Echinocactus platyacanthus* (Cactaceae) in the semiarid Central Mexico: Past, present and future. *Economic Botany* 45: 495–502.

Díaz del Castillo, B. 1991. *Historia Verdadera de la Conquista de la Nueva España (ca. 1568*). (F. Marenco, ed.). Editori Associati, Milan.

Donkin, R. A. 1977. Spanish Red. An ethnographical study of cochineal and the opuntia cactus. *Transactions of the American Philosophical Society* 67: 1–84.

Dressler, R. 1953. *The pre-Columbian Cultivated Plants of Mexico.* Botanical Museum Leaflets 16, Harvard University Press, Cambridge, Massachusetts.

Estrada, E. I. J. 1989. *El Códice Florentino, su Información Etnobotánica.* Colegio de Postgraduados, Chapingo, Mexico.

Felger, R., and M. Moser. 1983. *People of the Desert and Sea. Ethnobotany of the Seri Indians.* University of Arizona Press, Tucson.

Flannery, K. V., ed. 1986. *Guilá Naquitz.* Academic Press, New York.

Harlan, J. R. 1975. *Crops and Man.* Foundation for modern crop science series. American Society of Agronomy, Madison, Wisconsin.

Harlan, J. R. 1992 Origins and process of domestication. In *Grass Evolution and Domestication* (G. P. Chapman, ed.). Cambridge University Press, Cambridge, England. Pp. 159–175.

Hernández, F. 1959. *Historia Natural de Nueva España.* 7 volumes. Universidad Nacional Autónoma de México, Mexico City.

La Mantia, T., S. Cullotta, M. Marchetti, and S. Pasta. 2001. Materiali conoscitivi per una classificazione dei tipi forestali e preforestali della Sicilia. *L'Italia Forestale e Montana* 1: 24–47.

Le Houérou, H. N. 1996. The role of cacti (*Opuntia* spp.) in erosion control, land reclamation, rehabilitation and agricultural development in the Mediterranean basin. *Journal of Arid Environments* 33: 135–159.

Luna, C. 1999. *Etnobotánica de la Pitaya Mixteca (Pachycereae).* Ph.D. Thesis, Colegio de Postgraduados, Chapingo, Mexico.

MacNeish, R. S. 1967. A summary of the subsistence. In *The Prehistory of the Tehuacán Valley* (D. S. Byers, ed.). University of Texas Press, Austin. Pp. 290–231.

Martínez, M. 1993. *Catálogo de Nombres Vulgares y Científicos de Plantas Mexicanas.* Fondo de Cultura Económica, Mexico City.

Matos, E. 1994. Mesoamérica. In *Historia Antigua de México. Vol. I. El México Antiguo, sus Áreas Culturales, los Orígenes y el Horizonte Preclásico* (L. Manzanilla and L. López-Luján, eds.). Instituto Nacional de Antropología e Historia/Universidad Nacional Autónoma de México/Porrúa, Mexico City. Pp. 49–73.

Mattioli, P. A. 1558. *Commentarii in libro sex Pedacii Dioscoridis de Materia Medica.* Appresso V. Valgrisi, Venice.

Mattioli, P. A. 1568. *I Discorsi ne i sei Libri della Materia Medicinale di Pedacio Dioscoride Anarbeo.* Appresso V. Valgrisi, Venice.

Monjauze, A., and H. N. Le Houérou. 1965. Le role des *Opuntia* dans l'economie agricole nord-africaine. *Bullettin de l'École Nationale Superieure d'Agronomie de Tunis* 8–9: 85–164.

Nefzaoui, A., and H. Ben Salem. 2000. Opuntiae: A strategic fodder and efficient tool to combat desertification in the WANA region. *CactusNet Newsletter* 2000: 2–24.

Oviedo y Valdés, G. F. De. 1526. *Sumario de la Natural y General Historia de las Indias.* Ramon de Petras, Toledo, Spain.

Oviedo y Valdés, G. F. De. 1535. *La Historia General y Natural de las Indias.* Juan Cromberg, Madrid.

Pennington, C. 1963. *The Tarahumara of Mexico: The Environment and the Material Culture.* University of Utah Press, Salt Lake City.

Pimienta-Barrios, E., and P. S. Nobel. 1994. Pitaya (*Stenocereus* spp., Cactaceae): An ancient and modern fruit crop of Mexico. *Economic Botany* 48: 76–83.

Rebollar, A., J. Romero, P. Cruz, and H. Zepeda. 1997. *El Cultivo de la Pitaya (*Stenocereus *spp.), una Alternativa para el Trópico Seco del Estado de Michoacán.* Universidad Autónoma de Chapingo, Chapingo, Mexico.

Sahagún, B. 1970. *El Manuscrito 218–20 de la Colección Palatina de la Biblioteca Medica Laurenziana, Códice Florentino.* Gobierno de la República Mexicana, Mexico City.

Sahagún, B. 1985. *Historia General de las Cosas de Nueva España.* Porrúa, Mexico City.

Sahley, C. T., M. A. Horner, and T. H. Fleming. 1993. Flight speeds and mechanical power outputs of the nectar-feeding bat *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae). *Journal of Mammalogy* 74: 594–600.

Sánchez-Mejorada, H. 1982. *Las Cactáceas de México,* Secretaría de Desarrollo Agropecuario del Gobierno del Estado de México, Toluca.

Smith, C. E. 1967. Plant remains. In *The Prehistory of the Tehuacán Valley* (S. Byers, ed.). University of Texas Press, Austin. Pp. 220–225.

Smith, C. E. 1986. Preceramic plant remains from Guilá Naquitz. In *Guilá Naquitz* (K. V. Flannery, ed.). Academic Press, New York. Pp. 265–274.

Tangiorgi Tomasi, L., and A. Tosi. 1990. "*Flora e Pomona*," *l'Orticultura nei Disegni e Nelle Incisioni dei Secoli XVI-XIX.* Leo S. Olschki Editore, Florence.

Toledo, V. M., and M. J. Ordóñez. 1993. The biodiversity scenario of Mexico: A review of terrestrial habitats. In *Biological Diveristy of Mexico* (T. P. Ramamoorty, R. Bye, A. Lot, and J. Fa, eds.). Oxford University Press, New York. Pp. 757–777.

Valdes, B., Z. Diaz Lifante, and M. Martin Cacao. 1992. The introduction of American species through Seville past and present. *Museologica Scientifica* IX: 277–292.

Vargas, E. 1994. La frontera meridional de Mesoamérica. In *Historia Antigua de México,* Vol. 1, *El México Antiguo, sus Areas Culturales, los Orígenes y el Horizonte Preclásico* (L. Manzanilla and L. López-Lujan, eds.). Universidad Nacional Autónoma de México, Mexico City. Pp. 145–174.

CHAPTER

› 10 ‹

CACTUS PEAR FRUIT PRODUCTION

Paolo Inglese, Filadelfio Basile, and Mario Schirra

Introduction
The Cactus Pear Industry Worldwide
Supply and Demand Analysis
Selling Arrangements and Methods
The Cactus Pear Orchard
Site Selection
Cultivars
Orchard Design and Planting
Plant Training and Pruning
Fruit Thinning
Fertilizer Application
Irrigation
Fruit Characteristics
Harvesting
Productivity
Out-of-Season Crop
Quality
Postharvest Physiology
Conclusions and Future Prospects
Literature Cited

Introduction

Cactus pear (*Opuntia ficus-indica* [L.] Mill.) is cultivated for fruit production in both hemispheres and on all continents except Antarctica. The absence of updated statistical data from most countries in which this species is cultivated allows only a rough estimate of the worldwide land area used—about 100,000 hectares (ha) for specialized plantations. This figures does not include utilization of wild plants or those cultivated for self-consumption in home gardens or in small horticultural systems, which are common in Mexico (*nopaleras de solar*), Africa, the Middle East, South America (*huertos familiares*), and southern Europe (Mediterranean gardens).

During pre-Hispanic times, cactus pear fruits were especially popular among the indigenous populations of the arid and semiarid areas in their native Mexican highlands, and the fruit maintained its basic role in the local diet even



Figure 10.1. Pruning flowers and new cladodes of *Opuntia ficus-indica* via scozzolatura in June 2000, leading to a second bloom, in Santa Margherita Belice, Italy. The plantation of cultivar 'Gialla' is 10 years old, and the plants are spaced 4 m apart along rows that are 6 m apart.

after the Spaniards conquered the Aztec empire. Cactus pear reached the Mediterranean Basin during the 16th century. It became naturalized and the fruit was soon popular among the rural populations (Barbera 1995). At the beginning of the 19th century, commercial plantations were established on the island of Sicily (Barbera et al. 1992) to meet the increasing demand for late-ripening fruits, produced through *scozzolatura* (Fig. 10.1). This technique consists of removing the spring flush of flowers and cladodes to get a second bloom, causing the fruits to ripen in October to November (Northern Hemisphere), 2 to 3 months later than the summer crop (Barbera and Inglese 1993). These fruits were highly appreciated, not only by the rural population, but also by the middle class and the aristocracy of the Kingdom of Naples (Barbera 1995). More recent is the diffusion of the species as a fruit crop into Argentina (Ochoa 1997), California (Curtis 1977), Chile (Sudzuki et al. 1993), Israel (Nerd and Mizrahi 1993), and South Africa (Wessels 1988). In all these countries, cactus pears occur in naturalized stands and in commercial plantations for fruit production, both for subsistence agriculture and as a cash crop. This chapter outlines the basics of cactus pear cultivation, including economic features and postharvest fruit management.

The Cactus Pear Industry Worldwide

As indicated, statistics on the world area cultivated for cactus pear as well as its production, employment, and export figures are limited. The main producing country is Mexico, with a production of over 345,000 tons fresh mass year^{-1} on about 70,000 ha of specialized plantations, concentrated mainly in the north-central region—Zacatecas, San Luis Potosí, Aguascalientes, Jalisco, Guanajuato—and in the south-central region—Hidalgo, Mexico, Tlaxcala, and Puebla (Flores Valdez et al. 1995). Italy is the most important cactus-pear-producing country in the Mediterranean area, with about 3,500 ha of intensive plantations yielding about 70,000 tons (Basile and Foti 1997), and 15,000 ha overall. Sicily accounts for nearly all of the Italian production (Barbera and Inglese 1993). The area for intensive cactus pear plantations has expanded remarkably in the last few years, leading to 35,000 tons annually in 1975–78, 48,000 tons in 1987–90, and 63,000 tons in 1997–99. About 90% of the areas under intensive cultivation in Sicily are in three major production zones: the San Cono Hills, Santa Margherita Belice district, and the southwestern foothills of the Etna volcano.

The species was introduced to South Africa during the 17th century, and it became naturalized in the Cape region. Naturalized spiny or spineless cactus pear plants are most abundant in the Eastern Cape, where commercial cultivation is relatively unimportant. The Western Cape is South Africa's major deciduous fruit growing area, but there are few commercial cactus pear orchards, even though the potential seems good, provided some supplementary irrigation is possible in the summer. Recently, expansion of commercial orchards has occurred in the Northern Province and the Ciskey region, stretching from Gauteng Province to Mpumalanga (Brutsch 1997; Brutsch and Zimmermann 1993). The total area cultivated in South Africa is 1,000 ha, with an annual production of about 8,000 tons. In Chile, specialized plantations are cultivated in the Santiago metropolitan area, on about 1,100 ha, which supply over 8,000 tons of cactus pears. Cactus pear is cultivated to a lesser extent in Argentina (800 ha and 7,500 tons), Israel (300 ha and 6,000 tons), and the United States (200 ha and 3,600 tons; Bunch 1996; Ochoa 1997; Nerd and Mizrahi 1993). Specialized plantations for cactus pear exist in Brazil, Colombia, Peru, Spain, Greece, Turkey,

Jordan, Egypt, Tunisia (e.g., 16,000 ha recently planted near Kasserine), Algeria, and Morocco, but comprehensive statistics are not currently available.

Orchard management requires a high degree of hand labor, with poor potential for mechanization (Basile and Foti 1997). The labor costs, which do not include harvesting and the successive operations, range from 130 to 340 hours ha^{-1}, of which over 70% are due to pruning, fruit thinning, and scozzolatura (Fig. 10.1). Flores Valdez et al. (1995) report that fruit harvest and pest control account for most of the annual cost of a cactus pear orchard in Mexico, while postharvest management, including fruit marketing, account for 28 to 40% of the total cost. Profits, although positive, vary greatly in Italy as well as in Mexico and South America. The large number of commercial operators and the poor concentration of supply, together with poor distribution and marketing of the product, considerably restrain the market potential. To avoid further price drops due to an increase in the product's supply, proper marketing strategies must be adopted.

Supply and Demand Analysis

Demand for cactus pear in Italy is concentrated almost entirely from August to December. The reduced quantities consumed from March to May come from the Southern Hemisphere for those consumers seeking out-of-season fruits. In Italy, the demand for fruit from the summer crop and/or that belonging to a medium-low commercial category generally comes from low-spending-capacity consumers of cactus pears in the production zones themselves, and in those areas of northern Italy with high concentrations of southern and Sicilian emigrants, religious communities, and the armed forces. On the other hand, the demand for late-ripening fruits, obtained through scozzolatura, comes from medium-to-high-spending consumers, who associate the cactus pear with exotic fruit. Because the price of cactus pears has not fluctuated widely, the demand elasticity with respect to price is not known, although it is not elastic for low-quality fruits, and the demand for higher-quality fruit is more elastic. The cactus pear demand is relatively inelastic with respect to the earnings of consumers in lower social echelons and tends to be elastic for well-off consumers. In Italy, more than 25% of the cactus pears remain in Sicily, 20% go to foreign consumers, and more than 50% are consumed in other Italian regions, particularly where there are residents of Sicilian origin and emigrants from producing countries (such as North Africa), as well as pockets of high-spending consumers. In Mexico, the most important national markets are the large cities located in the north, as well as the medium-to-high-spending metropolitan consumers in Mexico City, Guadalajara, and Monterey (Flores Valdez et al. 1995).

The main factors that influence demand are: (1) presence of glochids and spines (which require adequate postharvest de-prickling management), (2) fruit color, (3) seed content, (4) size of the fruit, (5) time of ripening, (6) degree of maturity, and (7) packaging. Cactus pear demand has definitely grown both in Europe and elsewhere. Although no precise official statistical information is available, the trend is supported by increasing exports of the producing countries. Differences in the commercial ripening seasons and improvements in distribution have contributed to this product being consumed in many countries, over many months of the year. Indeed, at a world level, the complementary production of the Northern and Southern Hemispheres could potentially allow the fruit to be present on the market all year (Inglese 1994). Mexico exports 2,000 tons, mainly to the United States and Canada, where most of consumers are *Latinos.* Italy exports to Canada, the United States, and other European countries, such as France and Belgium and, to a lesser extent, to Germany, the United Kingdom, and Switzerland; consumers often come from Sicilian and other Mediterranean communities. Israel exports less than 100 tons per year, mainly to France, while South Africa exports an undefined amount of fruits to England and France. Chile and Argentina have a low export level to the United States and Canada.

The per capita consumption of cactus pears as fresh fruit is presently at about 2.5 kg $year^{-1}$ in Sicily, and fluctuates from a few hundred grams to 1 kg $year^{-1}$ for inhabitants of the other regions of Italy. Flores Valdez et al. (1995) estimate an annual consumption of 3.7 kg $year^{-1}$ in Mexico. Minimal demand occurs for cactus pear derivative products (jams, *mostarda,* ice cream, liqueurs, *queso de tuna, arrope*), which are mostly concentrated in the producing areas (Sicily and Mexico), within the producing families themselves, and for workers involved in the cultivation of the plant in production units. Most common is the self-production for personal consumption of these products, which also extends to confectionery craftsmanship. The development of this kind of product should play an important role in the cactus pear industry in the near future.

In Italy, 85 to 90% of the fruit is harvested, with fluctuations from year to year relating to undersized fruits, adverse meteorological conditions, and pathogens. More than 90% of the annual crop comes from the late fruits obtained by scozzolatura, whereas the summer crop is pro-

TABLE 10.1
Utilization and destinations of the cactus pear production in Italy, 1996–1999

Type	Average quantities	
	tons	*%*
Wholesale fruit and vegetable markets	28,500	45
Outside the market (street vendors, large chain distributors, etc.)	13,000	21
Foreign markets	12,000	19
Farm rejects, unsold stock, weight losses, and wastage	6,000	9
Personal consumption	3,500	6
TOTAL	63,000	100

duced only in old-fashioned orchards. The 'Gialla' cultivar accounts for 85% of the total production, followed by 'Rossa' (10%) and 'Bianca' (5%). About 75% of production is represented by "prime" and "secondary" quality fruit by weight (120–140 g); the "extra" (> 140 g) category is about 10 to 15%, and the rest is represented by "super-extra" (> 180 g) and "third" quality (< 120 g). Postharvest facilities and infrastructure are scarce, both in Italy and Mexico, and no more than 10% of the harvested crop is stored in cool chambers for 2 to 6 weeks. Despite the advantages gained from expanding the period of fruit marketing, there is a substantial lack of knowledge on postharvest technologies at a commercial level.

The main destinations for the cactus pear in Italy are the national wholesale fruit markets, followed by the "outside the market" and the foreign markets, rejects and wastage, and personal consumption (Table 10.1). The "outside the market" category is increasing, and consists mainly of street vendors. The owners of small holdings, who become the street vendors, sell their products at higher prices, especially in cities near the production zones. Small commercial operators serve consumer markets not covered by the local wholesale fruit and vegetable markets. The "outside the market" category also includes large-scale distribution chains, which sign contracts with commercial enterprises that have particular forms of packaging and guarantees of consistency. This category includes mass caterers (army canteens, hospitals, religious communities, university and large company canteens, schools, hotel complexes, and tourist villages), who find it more convenient to buy direct from producers in the period (autumn) when other fresh fruit is in short supply. Only modest quantities of cactus pears are currently absorbed by the confectionery, pharmaceutical, and cosmetic industries, although there is a definite growth potential.

Selling Arrangements and Methods

In Sicily, the most common means of selling cactus pears is ex farm. This form concerns about 80% of production, and the harvesting is paid for by the buyer. In some cases, the product is sold ex farm by weight, with harvesting being paid for almost exclusively by the producer. Less frequently the product is sold ex market, with the producer paying for harvesting, processing, and transport to the place of sale.

In the ex farm sale, the contract is verbally defined 2 to 3 months or more before harvesting and stipulates that the buyer pays 30 to 50% of the agreed-upon sum in advance, while the remainder is payable at the beginning of harvest. To determine the value of the goods, the quantity of goods to be produced that year is estimated, taking into account orchard age, layout, and management. Having agreed upon the production volume, the sales price is established; the buyer organizes the harvest of the product, spreading it out over time according to processing and storage capacities, as well as market trends. The relative production risks (e.g., climatic events) are transferred from the producer to the buyer at the moment of stipulating the contract. The buyer usually transfers the product to his own premises directly after harvesting, so processing and packaging can be completed as quickly as possible.

Sale ex farm by weight follows the same procedures regarding the nature and form of contract, advance payments, and forms of payment. The producer agrees with the buyer how many harvests will be produced for the buyer and sometimes also other aspects of the form and times of harvesting, with the general aim of allowing the buyer to find the best placing on the market for the product. Wide price fluctuations occur in sales by weight, so the buyer must take into consideration the categories of prod-

uct obtainable from the orchard, the care taken by the producer, and the varieties present. The risks linked to quality/quantity aspects of production remain with the producer until the goods are delivered. An ever-growing number of cactus pear producers prefer to sell *ex farm,* due to the reduced risks and the savings in time. A few producers, however, choose to sell their produce *ex market,* taking upon themselves all the operations to do with production, harvesting, processing, packaging, and, at times, storing of the cactus pears. This form is preferred by medium-to-large producers who have the necessary work force for the various phases of processing.

In some cases in Italy, the producer harvests the fruit and consigns it directly to the retailer; if the retailer is a street vendor, the product goes directly to the consumer. Some producer-dealers directly export the product, transporting it in trucks and/or ships for European destinations, or by air carrier toward other continents. Two main articulations of distribution are: (1) producer → wholesaler → retailer → consumer; and (2) producer → wholesaler → selling agent → retailer → consumer. Also, an intermediary (a mediator or buying agent) can act between the producer and the wholesaler.

For the processing of cactus pears, warehouses are equipped with fruit de-prickling machines plus selection and sizing belts. Selection, which entails eliminating undersized fruit and those damaged by flies, transport, or split by frosts and/or hailstorms, is carried out by specialized staff, who also ensure the working order of the machines. The product is packaged in plastic, wooden, or cardboard containers with a capacity of 3 to 5 kg. Until a few years ago, the wooden crate was the most common, whereas recently cardboard has become more common. According to its specific destination, the product can be packed in smaller 1 to 2 kg plastic, polystyrene, or cardboard cases.

Among the forms of sale of "packed" goods, selling directly in the warehouse prevails over selling through a selling agent or large distribution chains. The commercial enterprise that buys ex farm pays for the harvesting, transport of the product to the warehouse, processing, packaging, making up the pallets, and transport to the markets as well as for the commission charges. These costs together are U.S. $0.35 to $0.45 per kilogram. The commercial enterprises limit their marketing actions to illustrated pamphlets on the characteristics of the product, and on how to consume the product itself. A promotion/advertising campaign over several years has been activated by the Regional Government, with free tasting sessions of the fruit in the main sales outlets and in the restaurants of the larger Italian cities (Battaglia 1997). Prices at production in Sicily (Table 10.2), which refer to the fruit still on the plant with harvesting charged to the buyer, decreased in real terms by 25 to 30% from 1983 to 1999, mostly due to the expanding supply. This, together with a rise in production costs, has led to a drop in profits. The high values in 1986, 1994, and 1995 reflect high-quality cactus pears, indicating consumer preference.

TABLE 10.2
Average wholesale prices of cactus pears in the province of Catania, Sicily, 1983–1999

Year	Current Lira (£ kg^{-1})	1999 Lira Value (£ kg^{-1})	Index (1983–85 = 100)
1983	1,150	2,479	99
1984	1,280	2,495	100
1985	1,420	2,549	102
1986	1,900	3,214	128
1987	1,600	2,587	103
1988	1,800	2,773	111
1989	1,475	2,132	85
1990	1,353	1,843	74
1991	1,723	2,206	88
1992	1,878	2,280	91
1993	1,822	2,123	85
1994	2,701	3,029	121
1995	2,792	2,972	119
1996	1,787	1,830	73
1997	1,758	1,770	71
1998	1,740	1,721	69
1999	1,900	1,900	76

References: G. Timpanaro in Basile (1996) for 1983–1995 and the Chamber of Commerce, Industry, Craftwork and Agriculture of Catania for 1996–1999. These prices refer to late-ripening fruits, which were converted to constant currency using the coefficients calculated by ISTAT.

The Cactus Pear Orchard

Site Selection

Opuntias are cultivated in subtropical arid areas, with mild winters (average air temperature > 10°C) and hot summers, where the annual rainfall ranges from 100 to 600 mm, and with a well-defined dry season that may last 2 to 5 months. Where no rainfall occurs during fruit development, or where rainfall is annually less than 300 mm, cactus pear needs irrigation to ensure economic cropping. In most areas where cactus pear is cultivated for fruit production, the plant has a period of no visible meristematic growth. This period usually coincides with the winter, with its

short photoperiod and low temperatures. Indeed, high temperatures preceding bud differentiation reduce flower bud formation (Nerd et al. 1991; Nobel and Castañeda 1998), but the winter chilling requirement has never been quantified. On the other hand, cactus pear plantations for fruit production occur in the Canary Islands and in the valley of Catamarca in northwest Argentina, where less than 200 chilling hours accumulate during the winter.

In its native highlands of Mexico, cactus pear is cultivated in semiarid areas, where the annual rainfall is concentrated in the summer during the fruit development period. In the Mediterranean Basin, Middle East, North and East Africa, Argentina, California, and Chile, the dry season coincides with the long and hot summer, when vegetative and reproductive growth occur. For instance, cactus pear in Chile is cultivated in the Santiago metropolitan area, where the average monthly air temperature is 22°C in summer (January) and 10°C in winter (August). The dry season lasts 4 to 5 months, and annual rainfall averages 350 mm (Sudzuki et al. 1993). In Italy, the species is cultivated for fruit production in Sicily, where the climate is Mediterranean, with mild, rainy winters and hot, dry summers. The average annual temperature is 16°C, being 25°C in July/August and 15°C in October/November during fruit development. Annual rainfall is between 400 and 600 mm, with a 4-month dry season (June–September). In Israel, the species is cultivated in the Negev Desert, where the lowest average monthly temperature is 13°C in January and the highest temperatures (25°C) occur from June through October; annual rainfall ranges from 40 to 200 mm. In South Africa, the Eastern Cape and the Northern Province receive summer rainfall, and in the Western Cape rainfall is concentrated in the winter. The Northern Province and the Ciskey region are the most important areas for specialized plantations, and the earliest fruit crops come from the subtropical areas near the Tropic of Capricorn. These provinces have long, hot summers and mild winters, with an extremely uneven rainfall occurring mainly in the winter and less than 500 mm annually (Brutsch and Zimmermann 1993; Brutsch 1997). In all areas, the average annual temperature is above 15°C, average monthly temperature ranges from 10°C in winter to 26°C in summer, and from 14°C to 25°C during fruit development and ripening.

The species occurs over a wide range of soils. A soil depth of 60 to 70 cm ensures the development of the shallow root system. Soils with poor drainage, a high water table, or a superficial impermeable layer or hardpan should not be used for planting. Clay content should not exceed 20% to avoid root rotting and reduced root and canopy development. Cactus pear is not salt-tolerant; 50 to 70 mM NaCl should be considered the upper threshold for profitable growing.

Cultivars

Many species of the Cactaceae produce edible fruits (Chapters 9 and 11). Among the approximately 1,600 species in this family, the genus *Opuntia* has the most relevant role in agriculture. In the Mexican highlands, the center of genetic diversity for all opuntias (Pimienta-Barrios 1990; Mondragon-Jacobo and Pimienta-Barrios 1995), fruits come from wild plants of *Opuntia lindheimeri* Engel., *O. streptacantha* Lem., *O. megacantha* Salm-Dyck, and *O. joconostle* Web; *O. amyclaea* Ten. and *O. ficus-indica* are cultivated for fruit production on about 60,000 ha of specialized plantations (Pimienta-Barrios 1990). Natural hybrids are common in both cultivated and wild populations (Pimienta-Barrios and Munoz-Urias 1995). In South America, the United States, Africa, and the Mediterranean Basin, *O. ficus-indica* is the only species cultivated for fruit production. Spontaneous forms have a diploid ($2n = 2x = 22$) or a tetraploid ($2n = 4x = 44$) chromosome number, whereas cultivated varieties have a polyploid ($2n = 6x = 66$ or $2n = 8x = 88$) chromosome number in Mexico and Italy (Mazzola et al. 1988; Pimienta-Barrios and Munoz-Urias 1995).

Cultivars for fruit production can be distinguished by the color of the fruit peel and the ripe flesh, which can be red-purple, yellow-orange, white-cream, or greenish. Red, yellow, and white fruits are present in all the cultivated areas, but green fruits, with a greenish-white flesh, are found only in Chile and Peru (Mondragon-Jacobo and Pimienta-Barrios 1995). Cultivars also differ in plant shape, vigor, fertility, cladode and fruit size, fruit ripening time, seed count, and ability to reflower (Pimienta-Barrios 1990; Wessels 1988; Barbera and Inglese 1993). The largest diversity in plant shape occurs in the South African germplasm. Wessels (1988) describes bushy-type, columnar (long-cladode), and round-cladode plants, which also differ in terms of vigor, chilling requirement, and cladode fertility, and eventually require different orchard design in terms of plant spacing. The largest genetic diversity occurs in Mexico and South Africa, whereas in the other countries only a few cultivars have been described and are commercially cultivated. Nevertheless, within the same cultivar, different clones can be identified. For instance, in Italy and Argentina, at least 3 to 4 clones of the local 'Gialla' or 'Amarilla sin espinas' are distinguishable (Barbera and Inglese 1993; Ochoa 1997). Mexican cultivars show a great variability also in terms of fruit ripening time, with early

ripening cultivars harvested in May ('Tapona de Mayo' and 'Pachona') or June ('Naranjona') and late ripening ones are harvested in September ('Cristalina') or October to November ('Fafayuco,' 'Cascaron,' and 'Charola'). Italian, Argentinian, and South African varieties do not show any marked variability in fruit ripening time.

The most appreciated fruits in the international markets have a yellow-orange flesh, such as 'Gialla' in Italy, 'Amarilla huesona' in Mexico, 'Ofer' in Israel, 'Malta,' 'Gymnocarpo,' and 'Direkteur' in South Africa, and 'Amarilla sin espinas' in Argentina. Red-purple or pink fruits, such as 'Algerian' in South Africa, 'Rossa' in Italy, or 'Pelon liso' and 'Rojo pelon' in Mexico, are also highly appreciated, particularly in the United States, where the 'Andy Boy' cultivar with pink-red flesh is grown in California (Bunch 1996). Recent studies in Italy show that consumers unfamiliar with this fruit are attracted by red fruits, which they buy first (Asciuto et al. 1997; Battaglia 1997). Fruits with white or greenish flesh are prized only in regional or local markets, and their international trade is not large. White-flesh fruits are very sensitive to postharvest handling and to specific pests, such as *Ceratitis capitata* (the Mediterranean fruit fly).

Orchard Design and Planting

Cactus pear is commonly propagated via cuttings. The use of 1-year-old potted plants has been successful in South Africa (Wessels 1988) and Italy (Barbera et al. 1993a), but, although the field growth response is satisfactory (Inglese et al. 1996), additional costs are incurred for nursery establishment, plant transportation, and planting, making it barely feasible economically. Both single and multiple cladode cuttings are utilized.

Single cuttings can be 1 to 2 years old, and their surface area and dry mass have a significant influence on successful rooting and subsequent budding in the field. A surface area of 500 cm^2 or a dry mass of 70 to 100 g allow good plant growth (Barbera et al. 1993a; Inglese et al. 1996; Wessels et al. 1997). Other sources of variability of cladode rooting and subsequent plant growth in the field involve the age of the mother plant and its phytosanitary conditions, cutting planting depth, the cladode surface area left above-ground, soil temperature, and soil water content (Brutsch 1979; Wessels et al. 1997). Adventitious roots originate from phloem cells near the areole, while the cambium remains dormant. The stimulus to cell dedifferentiation and multiplication may occur within 2 days after the cuttings are placed in contact with the soil, and primordia emergence may occur within 14 days (Fabbri et al. 1996). The cutting may develop 60 g of root dry mass in the first year (Inglese et al. 1996). Cuttings are usually planted upright, with half of the cladode placed below ground.

A multiple cladode cutting is made of a 2-year-old cladode bearing, on its crown-edge, one or two 1-year-old daughter cladodes. The advantage for such multiple cladode cuttings is the rapid formation of plant structure, which results in earlier fruiting after planting. Similar results can be obtained by planting, in a single hole, two cuttings, spaced 0.4 m apart, or three to four cuttings placed in a triangle or square and spaced 0.3 m apart. This method ensures fast canopy development, but requires a large amount of planting material (Mondragon-Jacobo and Pimienta-Barrios 1995). Cuttings have to wilt 4 to 6 weeks in a dry, shaded environment before being planted to let the wound dry and prevent rot at the cut surface. Bordeaux paste, as well as 0.4 milliliter of methridathion or 1 g $liter^{-1}$ of copper oxychloride, are often applied to cuttings before planting.

Late spring is the best time for planting. Indeed, roots and cladodes reach their highest growth rate during late spring and early summer (Barbera et al. 1993a; Wessels 1988), and soil water content in late spring is high enough to allow root development in areas with winter rainfall, whereas cuttings benefit from rains that occur after planting in areas with summer rainfall (Pimienta-Barrios 1990; Barbera and Inglese 1993; Sudzuki et al. 1993; Wessels 1988). Planting at the end of the summer slows the development of the root system and canopy, due to low winter temperatures and reduced light (Barbera et al. 1993a); moreover, weeds compete more efficiently, and winter rains can promote root rot. If cuttings are planted during the hot and dry season without irrigation, root growth and budding are scarce, and cladodes readily wilt and eventually die because of high temperatures and low humidity. Even with summer rainfall, the time for rooting and cladode growth is often too short.

Good orchard design, in terms of plant layout and spacing, includes (1) hedgerow systems, with plants placed closely along a row, and (2) a square or rectangle layout, with plants trained to be globe-shaped and well separated from each other. Plantations established in Italy during the 19th century were laid out in hedgerows, with plants placed every 0.5 m along rows spaced 6 to 8 m apart (Barbera et al. 1992a). Orchards are established with a hedgerow layout in Israel and California (Bunch 1996), with cuttings placed at 1.5 to 4 m intervals along rows spaced 4 to 6 m apart (830–1,666 plants ha^{-1}). Pimienta-Barrios (1990) suggests a hedgerow layout for farms smaller than 5 ha, with close spacing (2–3 m) along rows spaced 5 m apart (1,110–1,666



Figure 10.2. View of the plantation considered in Figure 10.1.

plants ha^{-1}). Close spacing along a row increases the number of fertile cladodes per unit area in the early stages of orchard life. Close spacing results in continuous and dense canopies, which require a high pruning frequency and intensity to avoid within-plant shading and reduction of fruit quality. Canopies that are too dense reduce cladode fertility, facilitate cochineal infestations, and reduce the efficiency of pest control operations.

If the plants are spaced in a square or rectangular layout, they are usually trained to a bushy-type globe shape. In Italy, plant spacing ranges from 4 × 6 m (416 plants ha^{-1}; Fig. 10.2) to 5 × 7 m (290 plants ha^{-1}). In Mexico, Pimienta-Barrios (1990) recommends, for farms with more than 20 ha, distances of 4 m along rows spaced 5 m apart (500 plants ha^{-1}). In South Africa, plants are spaced according to the cultivar growth habit. Bushy-type plants develop a continuous hedgerow because of their open growth form. The general recommendation for bushy-type cultivars is 2 to 3 m along rows spaced 4 to 5 m apart (666–1,250 plants ha^{-1}). The upright types can be spaced 3 to 4 m apart along rows spaced 4 to 6 m apart (415–830 plants ha^{-1}; Wessels 1988). Because cladodes are generally planted with their planar surfaces parallel to the row direction, the rows should be oriented north-south to maximize light interception (Nobel 1988).

Plant Training and Pruning

Cactus pear plants can be trained to a globe shape of various sizes (height and width) or canopy densities based on cultivar growth habit, plant spacing, and environmental conditions. In many cases, plants are not trained and are pruned only occasionally. The globe-shaped plants have 3 to 4 main stems and a high number of fertile cladodes, mostly distributed around the outer portion of the canopy. Pruning can regulate resource allocation among the various canopy sinks and can maximize light availability within the canopy to support cladode growth, flower bud formation, and fruit growth. Moreover, pruning facilitates pest control, fruit thinning, and fruit harvest. Garcia de Cortázar and Nobel (1992) defined the stem area index (SAI) that maximises plant productivity in terms of biomass. High planting densities lead to an extremely high accumulation of dry matter into vegetative growth, but it reduces allocation to the fruit (Garcia de Cortázar and Nobel 1992).

This is the case for orchards for nopalito production (Chapter 13), which involve vegetative instead of reproductive growth. However, optimal SAIs for fruit production are unknown, as are strategies for annual and long-term pruning.

Even though pruning represents one of the major costs of orchard management, information on it is scarce (Basile and Foti 1997). Most net CO_2 uptake is by current-season and 1-year-old cladodes, with older cladodes serving as a pool of stored carbohydrates and nitrogen that can be used to support fruit and current-season cladode growth (Luo and Nobel 1993; Inglese et al. 1994b; Nerd and Nobel 1995). Flower buds differentiate on terminal, well-exposed 1-year-old cladodes, whose dry weight exceeds a minimum value for its surface area by at least 33 g (Garcia de Cortázar and Nobel 1992).

Moreover, cladode shading affects fruit growth in terms of size and ripening time (La Mantia et al. 1997). To avoid alternate year bearing, every year the plant must produce the same number of new cladodes, which will bear fruit 1 year later; new cladodes develop on 2-year-old and even older cladodes (Inglese et al. 1998a). Thus, to get an accurate seasonal balance between vegetative and reproductive growth, the plant needs a constant number of 1-year-old cladodes (for fruit production) and 2-year-old cladodes (for new cladode production). As a rule of thumb, to maximize their development, no more than two daughter cladodes should be retained on a parent cladode. Pruning also involves the removal of the current season's cladodes developing on fertile cladodes. Two-year-old cladodes, which have already produced fruit, should be removed if there is no vegetative activity. The number of fruiting cladodes left on a plant every year depends on plant spacing, and ranges from 100 to 120 for 350 to 400 plants ha^{-1} to 20 to 30 for 1,000 to 1,200 plants ha^{-1}. The closer the plant spacing, the higher the pruning intensity and frequency needed.

Pruning should be carried out when temperatures are high enough to make the cut dry out quickly, which prevents rot and scabies. Cladodes cut at their basal edge can be chopped and left between the rows. In South Africa, Wessels (1988) suggests pruning from May to July after the fruit harvest, when the plant is no longer actively growing. New cladodes will develop the following spring, a strategy feasible in regions with dry winters. In Mexico, Pimienta-Barrios (1990) suggests pruning from November to March, during the dry and cold season. Barbera and Inglese (1993) suggest that May to June is the best time for pruning. Plants should be topped at 2.0 to 2.5 m in height, which avoids the use of ladders for fruit thinning and fruit harvest.

Most plants have lower fruiting potential and cladode renewal 25 to 30 years after planting. At this stage renewal pruning can be an alternative to orchard replanting. Rejuvenation can be achieved by pruning the plants back to 4- to 5-year-old cladodes (Mulas and D'hallewin 1990). Heavier pruning back to the lignified cladodes can also be practiced to resume growth of weak plants. The plant generally resumes fruiting 2 to 3 years after such pruning, depending on the pruning intensity.

Fruit Thinning

The number of flower buds per fertile cladode varies according to cultivar (Barbera et al. 1991; Wessels 1992), season (Barbera et al. 1991; Nerd et al. 1993; Inglese et al. 1998a), cladode age (Inglese et al. 1994a, 1998a), and dry-weight accumulation (García de Cortázar and Nobel 1992). Cladodes bearing 3 to 7 flowers are the most common and account for 50 to 60% of plant fertility (Inglese 1994), but well-exposed cladodes might bear, along their crown-edge, 25 to 30 flower buds, most of them setting fruits. Net photosynthesis of developing fruits is limited, and its contribution to fruit carbon demand is greatest during the early stages of fruit development (8–10%; Inglese et al. 1994b). Fruits obtain most of their assimilates from their mother cladode, but the sink demand to support the growth of fruit and the current season's cladodes involves a substantial flow of stored carbohydrates from basal cladodes (Luo and Nobel 1993; Inglese et al. 1994). The carbon demand is greatest when more than six fruits develop on 1-year-old fruiting cladodes, and particularly during the last 3 to 4 weeks of fruit growth, when the flesh rapidly develops and accumulates sugars (Barbera et al. 1992b). At this stage, the import of photoassimilate is 30% and 70% of the fruit dry weight gain for cladodes with 5 and 15 fruits, respectively (Inglese et al. 1994b).

The fruit also competes with the current-season's developing cladodes, which show a higher growth rate than the fruit for most of the fruit development period. The fruit becomes a major sink during the final swell of the flesh, and this coincides with a consistent reduction in the growth rate of the current-season's cladodes (Inglese et al. 1999). Indeed, the fruit growth rate and harvest size decrease with fruit number per cladode, when more than six fruits are left on a cladode (Brutsch 1992; Inglese et al. 1995b). For South African cultivars, Wessels (1988) recommends retaining no more than 9 to 12 fruits per cladode to increase fruit harvest size. Cladodes with more than 10 fruits show irregular and delayed ripening. In areas with no rains during fruit development, thinning must be accompanied with irrigation to get a significant increase in fruit

size and percentage flesh (La Mantia et al. 1998). The effect of fruit thinning depends also on the number of fruits per cladode prior to thinning; the longer the time that the fruits are retained on a cladode, the greater the effect of the fruit number on final fruit size (La Mantia et al. 1998). Thinning can be performed from budbreak to the early stages of fruit development, but the most appropriate time is 10 to 20 days after bloom, when differences in fruit size are clear enough to allow selective thinning and flesh development is still negligible (Barbera et al. 1992b). Removing fruits 20 to 30 days after set reduces the effectiveness of thinning (Inglese et al. 1995b). Cladode size (surface area and thickness) and within-canopy position should also be considered to determine optimal thinning ratios.

Fertilizer Application

Unlike many other fruit crops, relatively little information concerning cactus pear nutrient demand and economy is available (Nobel 1988). Early investigations (Monjauze and Le Houerou 1965) demonstrate that manure application improves *Opuntia* biomass productivity. Similarly, fertilization with nitrogen (N) increases biomass production (Nobel et al. 1987), and phosphorous (P) application significantly increases fruit production (Gathaara et al. 1989). Cladode tissue N and potassium (K) concentrations are positively correlated, and sodium (Na) concentration are negatively correlated with fruit yield (Karim et al. 1998). Moreover, 1-year-old cladodes that produce new organs have a higher level of nitrate at the beginning of the season than do nonproductive cladodes (Nerd and Nobel 1995). The concentration of N in the parenchyma of fruiting cladodes decreases rapidly during fruit development, and K concentration is higher for nonproductive than for fruit-bearing cladodes. The magnesium (Mg) concentration is correlated with fruiting, but the calcium (Ca) content increases throughout the season, with no relation to cladode fertility (Inglese and Pace 1999).

Extensive N application soon after harvesting the summer crop promotes an additional budding in the autumn (Nerd et al. 1991, 1993), but it does not result in any increase in the main crop the following summer. Injection of KNO_3 promotes flower bud induction (Aguillar-Becerril 1994), and increased N concentrations in fertile cladodes reflect a rise in soluble reduced-N compounds, which is associated with flower bud production. Neither K nor P contents are correlated with the occurrence of the autumn flush of flower buds (Nerd et al. 1993). Fruit mass and soluble sugars increase with N fertilization, but high applied N (200 kg ha^{-1}) results in excessive vegetative growth (Potgieter and Mkhari 2000). Nitrate content is highest in the parenchyma and at the basal edge of the cladodes (Nerd and Nobel 1995).

Nutrient concentration in cladodes varies with age, position, fruit load, and season. Nitrogen concentration varies from 0.4 to 2.2%, with the highest values occurring in 2- and 3-year-old cladodes that serve as a reserve for the growth of new organs (Nerd and Nobel 1995; Inglese and Pace 1999; Potgieter and Mkhari 2000). Higher concentrations may result in excessive vegetative growth, a decrease in fertility, a delay in ripening, and a reduced fruit color. Claassens and Wessels (1997) obtained optimum fruit yield at a N concentration of 0.94 to 0.96%. Inglese and Pace (1999) found the highest fruit yield per cladode at 0.8% N. Concentrations of K and P reach 0.4 to 3.5% and 0.06% to 0.2%, respectively. Gathaara et al. (1989) found P and N fertilization to be beneficial to the yield of young plants of *Opuntia englemannii,* at least for the first year of growth.

Irrigation

Because of its high drought resistance and high water-use efficiency, cactus pear is usually cultivated without irrigation. However, in areas with no summer rains and where annual rainfall is less than 300 mm, the plants require supplementary irrigation to get adequate yields and good fruit quality (Barbera 1984; Mulas and D'hallewin 1997). Even in areas where summer rainfall of 300 to 600 mm is sufficient to ensure high yields and regular fruit development, dry winter conditions may result in late and poor flower bud induction, which in turn leads to late and low yields (Bowers 1996; Nerd et al. 1989; Van Der Merwe et al. 1997). Under these conditions, drip irrigation with daily, low amounts (1–2 mm day^{-1}) ensures high yields and good fruit growth. Moreover, light irrigation in early summer or during fruit swelling is desirable, particularly in light soils, to avoid wide variations in soil moisture, which promote fruit cracking (Wessels 1988). The counteracting effect of water deficit on fruit size increases with the number of fruits per cladode; on the other hand, irrigation alone cannot make up for reduced size when there are a high (> 10) number of fruits per cladode (La Mantia et al. 1998).

Where the species is intensively grown for fruit production, irrigation is common in areas with dry summers, particularly in Israel, Italy, and Chile. Both cladode fertility and fruit growth benefit. Barbera (1984) reports that two to three irrigations, with an annual amount of 60 to 100 mm, applied during the earliest stages of fruit development (within 40 days after bloom), increase yield, fruit

size, and flesh percentage. Irrigation may also increase seed weight and peel thickness (Mulas and D'hallewin, 1997); however, there is no clear influence on sugar content, fruit firmness, or flavor. In areas where vegetative growth occurs during the dry period, irrigation enhances plant development in terms of both cladode number and size (Mulas and D'hallewin 1997).

Traditional irrigation methods, such as basin irrigation, may result in extensive leaching and are not adequate because of the shallow root system of the plants. If irrigation is done only two to three times during the dry season, the use of furrows may be easy and inexpensive. Localized micro-sprinklers, which cover a relatively large soil surface area with small volumes, meet the characteristics of the shallow root system of cactus pear. Drip irrigation can be also utilized, particularly when irrigation is applied during most of the season, as in Israel. Seasonal volume ranges from 60 to 80 mm in Italy to 250 to 300 mm in South Africa to 500 mm supplied in Israel (Barbera 1984; Nerd et al. 1989; Van Der Merwe et al. 1997; La Mantia et al. 1998). NaCl in irrigation water should not exceed 25 mol m^{-3}. Na accumulates mostly in the roots, whereas, when using salty water, Cl content increases both in the roots and in the cladodes (Nerd et al. 1991).

Fruit Characteristics

Harvesting

The harvesting season for cactus pears lasts for a relatively long time. In the Northern Hemisphere, the main summer crop lasts from late June to mid September, depending on cultivar and environmental conditions. The earliest crop comes from North Africa and a late crop comes, in Italy, from October to November (Fig. 10.3), as a result of the removal of the main spring flush (Barbera et al. 1992a; Figure 10.1). A winter crop comes in Israel, following extensive fertilization and irrigation applied soon after harvesting the summer crop in July to August (Nerd et al. 1993). Extremely mild winter temperatures allow a prolonged harvest season for cactus pears in Salinas, California, where fruits are picked from September to March (Inglese 1995). In the Southern Hemisphere, the summer crop is harvested from December to February, with a second natural crop occurring from July through September in Chile (Sudzuki et al. 1993) and an artificially induced second crop that ripens in March to April in South Africa (Brutsch and Scott 1991). In the native areas of Mexico, the harvest season varies with environment and cultivar, and goes from May through October (Pimienta-Barrios 1990; Pimienta-Barrios and Munoz-Urias 1995).

The length of the fruit development period and the ripening time are cultivar-dependent but show large within-plant variability (Inglese et al. 1995a). Fruit ripening is asynchronous, even at a cladode level, and two or three pickings are required to harvest the entire crop. The harvest period of most cultivars may last for 2 to 6 weeks, depending on season and environment (Inglese 1994). The time of flower bud burst, cladode exposure to light (La Mantia et al. 1997), and fruit load per cladode (Inglese et al. 1995a) are the main sources of variability of the fruit ripening time at the plant level (Inglese et al. 1995a, 1999; La Mantia et al. 1997). Fruit development occurs over a wide range of climatic conditions throughout the world, including winter and summer seasons, and the time required to reach commercial harvest maturity varies from 70 to 150 days (Brutsch 1979; Pimienta-Barrios 1990; Nerd et al. 1991; Barbera and Inglese 1993; Inglese et al. 1999). On the other hand, the accumulated thermal time from bloom to commercial harvest is rather constant (40×10^3 degree hours), and different accumulation patterns of thermal time apparently account for the variability in fruit ripening time that occur by year and environment for the same genotype (Inglese et al. 1999).

Ripening is also sensitive to temperature. For example, high temperatures (> 25°C) result in a rapid onset of ripening that may affect fruit size and reduce postharvest durability, whereas low temperatures (< 15°C) delay fruit ripening time and result in a prolonged fruit harvest period at plant and orchard levels. When daily temperatures fall below 12°C, ripening slows and fruits may overwinter and ripen the next spring (Barbera and Inglese 1993). Temperatures above 35°C, and associated low air humidity, may cause sunburn damage on fruits (Brutsch 1992). Differences in temperatures during fruit development involve changes in fruit characteristics, such as size, shape, peel thickness and color, percentage flesh, sugar content, and seed count (Nerd et al. 1991; Barbera and Inglese 1993; Inglese et al. 1999). Fruit should be harvested when peel color changes, a time when the umbilical crown is still slightly green. At this stage, fruits can withstand a substantial storage and marketing period. At harvest, the concentration of reducing sugars is 90% of that for fully ripe fruits and should not be less than 13% by fresh weight; pulp firmness, as measured with an 8-mm cylinder, should not be less than 8 kg cm^{-2} (Pimienta-Barrios 1990; Barbera et al. 1992b). Fully ripe fruits are too soft to be stored and are difficult to handle.

Fruits should be harvested early in the morning, when their internal temperature is not higher than 25°C, and when the glochids are still wet and adhere to the peel. To

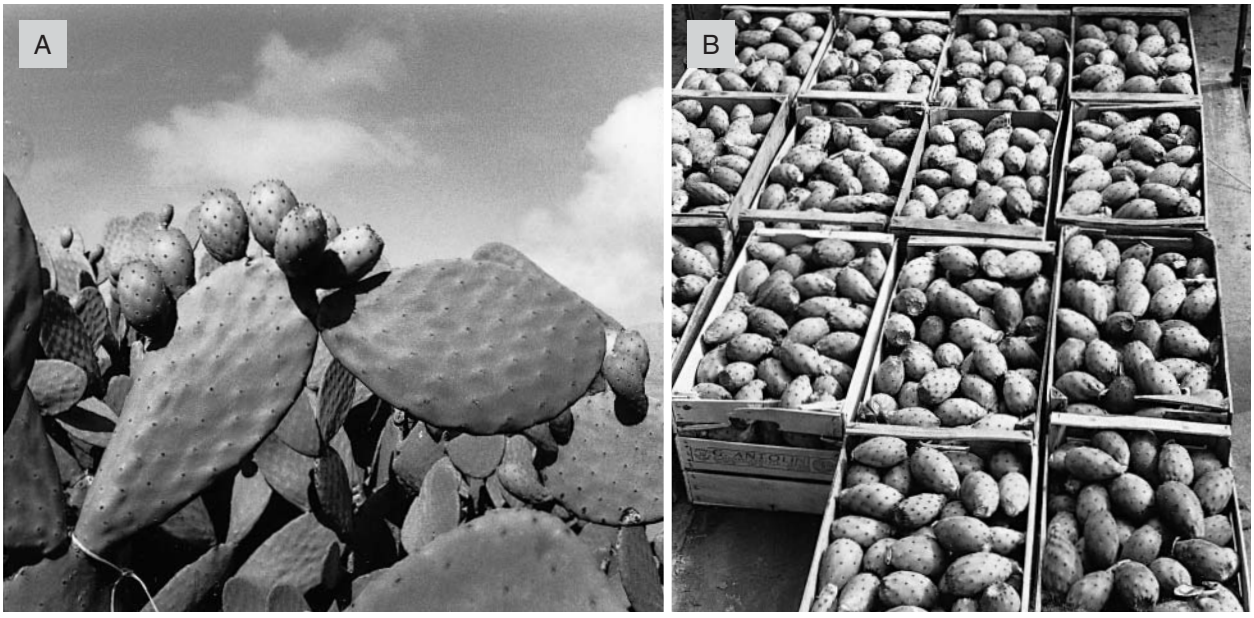


Figure 10.3. Fruit at harvest time at the end of October 2000 that resulted from scozzolatura (Fig. 10.1.): (A) fruits on cladodes and (B) fruits ready for transport from the field.

reduce postharvest decay caused by wound-infecting pathogens, fruits should be removed with a knife so as to leave a small piece of the mother cladode at the edge of the cut (Barbera and Inglese 1993). Subsequent exposure of fruits to room temperature (curing) is recommended to promote wound healing, the drying of the piece of cladode, and its ready detachment during handling and packaging (Chávez-Franco and Saucedo-Veloz 1985). Soon after harvesting, fruits are cleaned and brushed under a water spray or under suction to remove the glochids. Fruits are usually sorted according to size, color, shape, and overall appearance. Brushing involves rudimentary equipment, but it can be mechanized to increase efficiency and reduce fruit damage. Postharvest losses can be high, depending on cultivar, stage of maturity, environmental conditions, and harvesting method (Castillo-Castillo and Pimienta-Barrios 1990; Cantwell 1995; Schirra et al. 1999a).

Productivity

Fruit productivity of *Opuntia ficus-indica* is extremely variable from country to country. Yields of 20 to 30 tons ha^{-1} are reported in Israel and Italy (Barbera and Inglese 1993; Nerd and Mizrahi 1993) and 10 to 30 tons ha^{-1} in South Africa (Wessels 1988; Brutsch and Zimmerman 1993). Much lower yields occur in Chile, 6 to 9 tons ha^{-1} (Sudzuki et al. 1993), and Mexico, where yields range from 4 tons ha^{-1} in the north to 9 tons ha^{-1} in the central area (Federal District) and 20 to 25 tons ha^{-1} in the south (Pimienta-Barrios 1990; Flores Valdez et al. 1995). In Israel, Nerd and Mizrahi (1993) report fruit yields of 18 tons ha^{-1} for a 4-year-old orchard with plants spaced 4 × 1.5 m apart. In the Salinas Valley of California, Bunch (1996) reports an average of 12 tons ha^{-1}, with peaks of 25 tons ha^{-1}, for planting densities of 370 to 430 plants ha^{-1} (plants spaced 6 × 4 m or 6 × 4.5 m). Impressive yields have been measured for young *O. ficus-indica* cv. 'Gialla' plantations in Argentina (Catamarca), where climatic conditions allow extremely fast plant development (P. Inglese, personal observation). The wide variability in yield depends on orchard design (plant spacing), cultural practices, environmental conditions (including soil type), and cultivar fertility.

Productivity also varies at the plant level. Differences in planting material, related to the rooting ability of cuttings and subsequent canopy development, account for discrepancies in yield potential 4 or 5 years after planting (Brutsch 1979; Wessels et al. 1997). Biennial bearing—with differences of 40 to 50% in fruit yield between off and on years—has been reported in Italy (Barbera et al. 1991), Mexico (Pimienta-Barrios 1990), and South Africa (Brutsch 1979), and also for natural stands of *Opuntia engelmannii* in the Sonoran Desert (Bowers 1996). Mismanagement of pruning (Inglese et al. 1998a), plant age, and interactions between developing fruits and flower buds (Barbera et al. 1991) or vegetative versus reproductive growth (Bowers 1996) may account for this behavior.

Plants begin to yield 2 to 3 years after planting, reach their maximum potential 6 to 8 years after planting, and bear for 25 to 30 years or even longer, depending on pruning and overall orchard management. For a mature plant, most (80–90%) 1-year-old terminal cladodes bear fruit and account for 90% of the annual yield. However, they show a wide fertility range, depending on plant age, environmental conditions, and their state of growth, as indicated by the accumulation of dry matter relative to the cladode surface area (Garcia de Cortázar and Nobel 1992), their orientation and exposure to light, and vegetative versus fruit competition (Inglese et al. 1999). Two-year-old cladodes are less fertile than 1-year-old ones; they usually account for no more than 10% of the commercial yield, but may become an important source of fruits in the off years and in older plants; they have a poor ability to reflower, and their fertility usually does not exceed 6 to 10 fruits per cladode (Nerd et al. 1993; Inglese et al. 1994a; Inglese et al. 1998a). However, 80 to 95% of the vegetative buds, which will become fruiting cladodes 1 year after formation, differentiate on 2-year-old cladodes (Inglese et al. 1998a).

Strategies to increase productivity involve management to raise the number of fertile cladodes per plant and increasing the planting density. To get an annual yield of 20 tons ha^{-1}, given a cladode fertility of 6 fruits and a fruit size of 100 to 120 g, 28,000 to 30,000 fruiting cladodes are needed per hectare. This means 80 to 90 fertile cladodes on bush-type plants placed 6 × 5 m apart (335 plants ha^{-1}) or 28 to 30 fertile cladodes per plant for high density, hedgerow-like orchards with plants spaced at 5 × 2 m (1,000 plants ha^{-1}). Dry matter partitioning of mature, fruiting cactus pear plants indicates a seasonal competition between vegetative and reproductive growth, involving fruits, newly developing cladodes, and the secondary growth of older cladodes. Current season's cladodes are the strongest sink for most of their growth period, but the fruit becomes the strongest sink during the last stage of fruit growth; secondary growth is the weakest sink, and old cladodes can contribute to the carbon budget through the remobilization of their stored carbohydrates (Luo and Nobel 1992; Inglese et al. 1994b). Seasonal values of harvest index, a term indicating the relative partitioning of current season's dry matter to the fruits, range from 35 to 46% (excluding root growth) and are similar to those reported for deciduous fruit crops. This demonstrates, once again, the high efficiency of cactus pear as a fruit tree.

Out-of-Season Crop

One of the most striking features of *Opuntia ficus-indica* is certainly the ability of its cladodes to reflower at different times, naturally or after inductive practices are applied (Nerd and Mizrahi 1997). In Chile, terminal cladodes reflower naturally in May to June, and the resulting second crop comes in July to September, with 50 to 60% lower yield than the major summer crop (Saenz Hernandez 1985; Sudzuki et al. 1993). An autumn crop also occurs in the Santa Clara Valley of California, with fruit ripening in winter and spring (Curtis 1977; Bunch 1996). In Israel, the off-season crop develops on the current season's terminal cladodes that bear fruit a few months after extensive N fertilization (80–120 kg ha^{-1}) and irrigation applied soon after harvesting the summer crop in July; the amount of this crop is rather low (20–30% of the summer crop), and decreases with plant age (Nerd et al. 1993). In Italy (Barbera and Inglese 1993; Inglese 1994) and South Africa (Brutsch and Scott 1991), a second flowering is obtained as a result of the complete removal of the spring flush of flowers and cladodes. In this case, a plant produces once a year, whereas in Chile the natural reflowering allows for two crops per year.

The spring flush removal (scozzolatura, Fig. 10.1) takes place when the main bloom occurs, between the end of May and the last week in June in the Northern Hemisphere, and in October in the Southern Hemisphere. The new flower buds develop on the fertile cladodes of the natural flush, and the reflowering index, defined as the ratio of second versus first flush flowers, is highest for cladodes with a natural fertility of 5 to 10 flowers. The reflowering index sharply decreases with the number of flowers in the first flush (Inglese 1994). Removal time affects the cladode reflowering rate (Barbera et al. 1991; Brutsch and Scott 1991). Removing flowers at a pre-bloom stage results in the highest reflowering rate, whereas removing the spring flush after petal shedding reduces reflowering by 50 to 70% (Barbera et al. 1991; Inglese et al. 1998b). This decrease in reflowering, which occurs when flowers are removed at full bloom or after petal shedding, is related to an inhibitory effect on flower bud initiation (Barbera et al. 1993b) caused by gibberellic acid (GA_3) diffusing from the flowers to the mother cladode (Inglese et al. 1998b). Indeed, Barbera et al. (1993b) demonstrate that GA_3 applied within 6 days after the spring flush removal completely inhibits reflowering, indicating that the flower bud, induced the preceding spring (Cicala et al. 1997), is still in a reversible stage. The current season's developing cladodes also inhibit reflowering if they are not fully removed (Inglese et al. 1994a).

Fruits induced by removing the first flush flower buds have the shortest development period, ripening 15 to 20 days earlier than full-bloom fruits and 30 to 40 days earlier than fruits induced after removing post-bloom fruits.

The reflowering rate also depends on the environmental conditions at removal time, especially soil water content and air temperature. Indeed, the extent of reflowering greatly differs from year to year and with orchard location (Barbera et al. 1991; Brutsch and Scott 1991; Nieddu and Spano 1992). To improve reflowering in light soils with low water content, irrigation should be applied at the moment of spring flush removal. Scozzolatura should not be applied until 3 to 4 years after planting, when reflowering ability is still poor.

Quality

Fruit quality varies with cultivar and depends on several management, environmental, and physiological factors. Fruit growth potential is determined by effective pollination, hence seed count (Barbera et al. 1994; Pimienta-Barrios 1990, Nerd et al. 1991), but factors such as light (La Mantia et al. 1997), water availability (Barbera et al. 1998), temperature (Inglese et al. 1999), cladode fruit load (Wessels 1988; Brutsch 1992; Inglese et al. 1995b), and interactions between developing fruits and cladodes (Inglese et al. 1994b, 1999) may also play a substantial role in determining fruit growth potential, final fresh weight, and other quality attributes. Pruning, fruit thinning, and irrigation are the most powerful tools to maximize fruit size. Average fruit fresh weight varies with cultivar, from 100 to 240 g. Mexican cultivars such as 'Cristallina' and 'Burrona' may reach 240 g in fresh weight (Pimienta-Barrios 1990), whereas fruit weight of the Italian 'Gialla,' 'Bianca,' and 'Rossa' generally ranges from 100 to 160 g (Barbera and Inglese 1993). In South Africa, fruit fresh weight of cactus pear ranges from 100 g ('Algerian') to 180 g ('Nudosa'; Wessels 1988).

Export size fruit must exceed 120 g. The percentage of flesh, which should not be lower than 55%, is less variable than fruit size (Inglese 1994; Inglese et al. 1994a). It ranges from 60 to 65% for the Italian cultivars ('Gialla,' 'Bianca,' and 'Rossa'), but a wider range has been found in South Africa (Wessels 1988). In Mexico, a comparison between nine cultivars revealed a 40 to 60% range in size (Pimienta-Barrios et al. 1992). Low temperatures during fruit development promote an increase in peel thickness and a reduction of flesh growth, resulting in a low flesh:peel ratio (Nerd et al. 1993; Barbera and Inglese 1993).

Sugars, mainly glucose (6–8% on a fresh weight basis) and fructose (5–6%), accumulate rapidly when the flesh begins to grow, and harvest values should be at least 13% (Barbera et al. 1992). The genotype is the main source of variability in sugar content, with some Mexican varieties reaching 17 to 18% (Pimienta-Barrios 1990), while crop load or fruit position within the canopy do not affect sugar content as much. Low temperatures during fruit development result in a significant reduction of sugar content at harvest (Barbera et al. 1991; Nerd et al. 1993). Organic acid content is very low (0.03–0.12%, expressed as malic acid), and the pH ranges between 5.0 and 7.0 (Barbera et al. 1992b; Kuty 1992).

Seed number and the ratio between empty and normal seeds are among the most important factors defining fruit quality. Seed number per fruit ranges from 120 to 350, and the empty versus normal seed ratio is higher in Italian (0.44) than in Mexican (0.11) cultivars (Barbera et al. 1994). Seed weight changes with cultivar, ranging from 2.0 to 7.0 g per fruit (Parish and Felker 1997). The nutritional value is similar to peach fruit (150 kilojoule per 100 g fresh weight of digestible fraction). The ascorbic acid content is 20 to 30 mg per 100 g (Inglese 1994).

Postharvest Physiology

Cactus pear is a non-climacteric fruit with low respiration and ethylene production rates (Lakshminarayana and Estrella 1978; Lakshminarayana et al. 1979; Cantwell 1995), although a preharvest climacteric-like rise in respiration rate has been observed in fruit harvested at different stages of development (Moreno-Rivera et al. 1979). Cantwell (1995) indicates that fruit harvested at green, intermediate, and ripe stages produces similar levels of CO_2, but sharp increases in respiration and ethylene rates are usually detected when fruits are removed from cold storage and placed in shelf-life simulating conditions (Schirra et al. 1997a,b). This also depends on ripening status and storage duration (Schirra et al. 1999b). Postharvest changes of internal quality characteristics, such as pH, titratable acidity, soluble solids, acetaldehyde concentration, and ethanol concentration in the flesh, are low, whereas ascorbic acid concentration may decrease, depending on storage conditions.

The postharvest life span of the fruit is relatively short. Under shelf-life conditions, cactus pear fruits may deteriorate in a few weeks as a result of rapid aging and decay. However, in the 19th century, when adequate storage facilities did not exist, fruits wrapped with thin paper were preserved in dark, cool rooms for 3 to 4 months (Bazin 1979). Covering them with straw helps reduce the water loss rate. Rodríguez-Félix et al. (1992) found that a total water loss of about 8% affected the fruit's overall visual appearance. Fruit brushing to remove glochids adversely affects keeping quality and increases the rate of water loss and decay (Testoni and Eccher-Zerbini 1990). Common postharvest pathogens of cactus pears include fungal infections (e.g., with *Alternaria* spp., *Botritis* spp.,

Chlamydomyces spp., *Fusarium* spp., *Penicillium* spp.) and bacterial infections (Chessa and Barbera 1984; Rodriguez-Felix et al. 1992; Chapter 14).

Like most tropical and subtropical fruit species, when stored at temperatures below 8°C, cactus pears are susceptible to physiological disorders collectively known as chilling injury, which involve the appearance of dark spots on the peel (Chessa and Barbera 1984; Cantwell 1995). Such postharvest responses depend upon growing conditions, cultivar, and fruit ripening stage at harvest. For example, fruit of 'Verde' cultivated in Chile is resistant to chilling injury, as no visible symptoms occur after 2 months of storage at 0°C (Berger et al. 1978), whereas fruits of *Opuntia amyclaea* and *O. ficus-indica* from Chapingo, Mexico, have chilling injury when stored at 8 to 10°C for 15 days (Chavéz and Saucedo 1985), and those of 'Gialla' grown in Italy exhibit severe injury after 14 days at 6°C (Chessa and Barbera 1984; Chessa and Schirra 1990).

Preharvest spraying with gibberellic acid increases fruit resistance to decay during cold storage but promotes susceptibility to chilling injury (Schirra et al. 1999a). Scanning electron microscopy indicates that this effect is related to a delay in peel maturation (Schirra et al. 1999b), and similar effects occur following preharvest sprays with 20 g/liter CaCl (Schirra et al. 1997b, 1999b). Fruits harvested at color change are less susceptible to decay but more prone to chilling injury than are fully ripe ones (Gorini et al. 1993). Fruits that ripen under high temperatures and low relative humidity are highly susceptible to chilling injury but less sensitive to rot decay, whereas fruits ripening at the onset of the rainy season under lower temperature are sensitive to rot but less susceptible to chilling (Schirra et al. 1999b). The rate of water loss increases during cold storage and the subsequent marketing period—and more rapidly so in summer than in autumn fruit, presumably because of a more rapid rate of metabolism resulting from the higher summertime temperatures (Monselise and Goren 1987). The sharp increases in weight loss when fruits are moved from chilling to non-chilling temperatures have been related to microscopic cracks in the rind (Cohen et al. 1994), on which decay depends during the marketing period.

Keeping the fruits in ventilated cold rooms at 6 to 8°C and 90 to 95% relative humidity is generally recommended for a storage life of 3 to 4 weeks (Gorini et al. 1993; Chessa and Barbera 1984; Cantwell 1995). This is the best compromise among preventing chilling injury, controlling decay, reducing respiration, and reducing transpiration. Upon longer storage, losses from rot and/or chilling injury may increase sharply, especially when the fruits are transferred from cold storage to the market. Chessa and Barbera (1984) found an 84% decay of autumn 'Gialla' fruit after a 60-day storage at 8°C, dropping to 67% at 5°C. Decay was caused by *Alternaria, Fusarium,* and *Penicillium* spp., and, to a lesser extent, by bacterial infections. Storage under intermittent warming to 8°C for 4 days for every 10 days at 2°C reduces chilling injury and decay after 6 weeks of refrigeration followed by 1 week at 20°C compared to storage at a constant 6°C (Chessa and Schirra 1990). Storage at cycles of 3 weeks at 2°C followed by 1 week at 8°C halves decay compared to continuous storage at 5 or 8°C (Gorini et al. 1993).

Storage at 5°C under a controlled atmosphere of 2% O_2 and 2% or 5% CO_2 reduces fruit decay by approximately 77%, alleviates chilling injury, and decreases water loss, thus resulting in fruits of enhanced appearance compared to those in a standard atmosphere (Testoni and Eccher-Zerbini 1990). Packaging with heat-shrunk polyethylene film remarkably reduces fruit weight loss, alleviates chilling injury, and results in better appearance but does not reduce decay during 6 weeks of storage at 6°C and subsequent marketing at 20°C (Piga et al. 1996). Wrapping with polyolefinic film retains fruit freshness and greatly reduces fruit weight loss during 4 weeks of storage at 9°C and subsequent marketing (Piga et al. 1997).

Postharvest dip treatments with conventional fungicides, such as benomyl, captan, and vinclozolin, are ineffective in controlling postharvest decay of cactus pear fruit, although thiabendazole (TBZ) effectively suppresses decay development and mitigates expression of chilling injury (Gorini et al. 1993). Dip treatments (2 minutes) with a heated (48–50°C) mixture containing 250 mg/liter benomyl and 1050 mg/liter betran reduces decay during 8 weeks of storage at 0°C and 80 to 85% relative humidity (Berger et al. 1978). The increased efficacy of heated fungicides reflects enhanced fungicide uptake and better coverage (Cabras et al. 1999). Fruit dipping in 1 mg/liter TBZ at 55°C for 5 minutes significantly reduces cold- and rot-induced losses in late-crop fruits during 4 weeks of storage at 6°C followed by 1 week of marketing at 20°C, without causing heat injury or detrimental effects to fruit firmness, flavor, taste, or peel appearance (Schirra et al. 1996). Similar results are observed following dipping in hot water, which also helps remove glochids—known causes of numerous micro-lesions in the skin that represent possible entry points for wound pathogens.

Hot air treatment for 24 hours at 38°C and > 95% relative humidity reduces chilling injury (Schirra et al. 1996). For summer fruits, such a hot-air treatment reduces decay fourfold, whereas a 48- or 72-hour treatment prior to 3 weeks at 6°C and 1 week at 20°C halves the decay

TABLE 10.3
Recommendations for maintaining postharvest fruit quality

Maturity indices	Peel color change (breakage) from green to yellow or red, fruit firmness, flattening of floral cavity
Quality indices	Total soluble solids (minimum of 13%, maximum of 17%, depending on cultivar), pH (6.0–6.5), tritatable acidity (0.03–0.12%), firmness (10–12 kg cm^{-2}), percent flesh (50–60%), fruit size (minimum of 120 g, maximum of 240 g, depending on cultivar)
Optimum storage temperature	6 to 8°C with a storage potential of 2 to 6 weeks, depending on cultivar, ripeness stage, and preharvest environmental conditions
Optimum relative humidity	90 to 95%
Fruit respiration rates	Nonclimacteric, with low respiration rate (15–20 ml CO_2 kg^{-1} $hour^{-1}$ at 20°C)
Physiological disorders	Chilling injury, when exposed at temperatures below 5°C for more than 24 hours (pitting and dark brown spots on the peel surface)
Pathological disorders	Fruit decay may result from peel or stem-end damage occurring during harvest and storage, or after glochid removal; main agents are *Alternaria* spp., *Dothiorella ribis,* and *Penicillium* spp.
Postharvest heat treatment (hot water dips or curing)	Conditioning fruits at 37 to 38°C for 24 to 48 hours reduces chilling injury; prestorage dipping in water at 50 to 55 °C for 3 to 5 minutes reduces decay

Adapted from Kader (1999).

(Schirra et al. 1997a). The hot air treatments lead to better external fruit appearance and a lower weight loss, especially for fruits treated for 48 or 72 hours. Ascorbic acid levels are generally lower in all fruits following a simulated shelf life.

The role played by heat treatments in decay control has been related to an inhibition in spore germination and growth, a delay that may allow the fruit to build up resistance at the wound site, and a stimulation of host-defense responses, such as acceleration of wound healing, induction of heat shock proteins, eliciting of antifungal compounds, membrane stabilization, and changes in enzyme activity (Lurie 1998). Ultrastructural studies have shown that the skin surface of mature fruit displays areas with wax layers in the form of plate-like structures (Chessa et al. 1992; D'hallewin et al. 1999) and micro-lesions in the skin caused by glochids during fruit handling (Schirra et al. 1999b). Postharvest treatments with water at 50°C for 2 minutes or heat treatment for 24 to 72 hours at 37°C and > 95% relative humidity apparently fuse and remodel the epicuticular wax (D'hallewin et al. 1999; Schirra et al. 1999b)—most platelets flatten and gaps, micro-lesions, and stomata appeared partially or completely filled with melted wax (Schirra et al. 1999b). Furthermore, early germinating spores are covered and mummified by the molten wax. Thus, beneficial effects of heat treatments on decay control may be due to the melting and remodelling of epicuticular wax layers and the subsequent filling of possible entry points for wound pathogens. Table 10.3 summarizes recommendations for maintaining fruit quality during postharvest management.

Conclusions and Future Prospects

Since the 16th century, opuntias in general and *Opuntia ficus-indica* in particular have been utilized in subsistence and market-oriented horticulture of many communities in dry areas of Africa, Asia, Europe, North America, and South America. However, fruit consumption is still mostly limited to local or ethnic markets, with poor export flows (Basile and Foti 1997). Indeed, the cactus pear industry only reaches an important size in Mexico, which accounts for 70% of the cultivated area worldwide, whereas in Argentina, Chile, Italy, South and North Africa, and the United States, the cactus pear fruit industry is limited to areas where natural resources do not allow the cultivation of most alternative fruit-tree crops.

Two questions arise: What limits the horticultural potential of this species? and How can cactus pear fruit consumption be encouraged? Despite the efforts made in the last 15 to 20 years, horticultural knowledge on this species is still scarce, and technical and scientific information available to farmers is limited. As a result of poor and nonstandardized orchard management, great discrepancies in yield within countries persist. Yet, rational and sustainable orchard management makes possible the improvement and standardization of yields and fruit quality. To improve fruit productivity and quality, knowledge of the environmental influence on plant fertility, fruit growth, and ripening must

be increased. Moreover, the existing genetic resources (cultivars) should be characterized in terms of ecological adaptation, fertility, productivity, ripening time, and fruit characteristics.

The major factor limiting the horticultural potential of cactus pear is the poor economic value of its fruits, which, although appreciated in rural communities, still fail to appeal to the urban consumers of the rich European and North American markets. Marketing and promotional campaigns as well as consumer education should be promoted at local and international levels. An efficient distribution structure should be encouraged through international cooperation. Moreover, fruit quality standards need to be set, and fruit quality enhanced through appropriate orchard design and management, primarily irrigation, fruit thinning, plant pruning, and consideration of cladode orientation.

The presence of glochids in the peel and the hard, thick seeds in the flesh are the major constraints for an enhancement in cactus pear consumption. Glochids can be removed effectively soon after harvest, but technologies must be improved and consumers need to be educated. Eventually, selection and breeding for glochid-free cultivars should be accomplished. The reduction of seed content is a major challenge for future research. Growth regulators (e.g., GA_3 sprays) have been utilized to induce embryo abortion and seed failure (Gil and Espinosa 1980), with controversial results leading to poor chances for application on a commercial scale. The large variability of seed number and the frequency of stenospermic seeds in many cultivated varieties provide good opportunities for selection and breeding. Seedless selection of *O. ficus-indica* cvs. 'Gialla' and 'Ofer' have been described (Barbera and Inglese 1993; Weiss et al. 1993), but they cannot be grown profitably because of the reduced growth of the edible portion. Damigella (1958) described a spiny selection of *O. amyclaea* Ten. var. *leucosarca,* which is seedless, because more than 90% of its seeds are stenospermic; its white-flesh fruits are regular in size and the percentage of flesh is 50 to 55% (P. Inglese, personal observation).

Various physical and chemical approaches have been investigated to improve the shelf quality of cactus pear fruit. The maximum benefit is achieved when fruit is of top quality, harvested when properly ripe and free of defects. Moreover, packaging lines, storage facilities, transport systems, and marketing channels must be kept clean and sanitary so as not to thwart efforts made to maintain high fruit quality. To replace or to minimize treatments with synthetic chemicals, research efforts are currently focused on enhancement of host resistance to pathogens via physical, chemical, or biological inductors. Besides physical methods, heat treatments (such as hot water dips and curing) are currently recognized as possible controllers of postharvest diseases by direct inhibition of the pathogen and by stimulating several host-defense responses. Yet, while conventional fungicides are the most effective and practical means for controlling postharvest decay of cactus pear fruit at present, the potential of fungicides when applied at 50 to 53°C may represent a viable approach in the future, with clear economic and environmental advantages.

Finally, international cooperation and technical assistance has given excellent results in recent years. This is the case of the efforts of international organizations, such as the Food and Agriculture Organization of the United Nations, which helped the establishment in 1993 of the International Network for Technical Cooperation on Cactus Pear (CactusNet-FAO), with scientific members from more than 20 countries (Pimienta-Barrios et al. 1993), and the Professional Association for Cactus Development (PACD), which involves scientists, growers, and professionals in the promotion of cactus pear utilization and fruit consumption worldwide.

Literature Cited

Aguilar-Becerril, G. 1994. Response of prickly pear (*O. ficus-indica* Mill.) to the injection of agrochemicals, frost injury and root pruning. *Revista de Fitotecnología Mexicana* 17: 186–193.

Asciuto, A., T. Cirivello, and M. Crescimanno. 1997. Production and market aspects of cactus pear cultivation in Italy. *Acta Horticulturae* 438: 159–170.

Barbera, G. 1984. Ricerche sull'irrigazione del ficodindia. *Frutticoltura* 46: 49–55.

Barbera, G. 1995. History, economic and agro-ecological importance. In *Agroecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 1–11.

Barbera, G., and P. Inglese. 1993. *La Coltura del Ficodindia.* Calderini Edagricole, Bologna.

Barbera, G., F. Carimi, and P. Inglese. 1991. The reflowering of prickly pear *Opuntia ficus-indica* (L.) Miller: Influence of removal time and cladode load on yield and fruit ripening. *Advances in Horticultural Science* 2: 77–80.

Barbera, G., F. Carimi., and P. Inglese. 1992a. Past and present role of prickly-pear *Opuntia ficus-indica* (L.) Mill. in the agriculture of Sicily. *Economic Botany* 46: 10–20.

Barbera, G., F. Carimi, P. Inglese, and M. Panno. 1992b. Physical, morphological and chemical changes during fruit development and ripening in three cultivars of prickly pear *Opuntia ficus-indica* (L.) Miller. *Journal of Horticultural Science* 67: 307–312.

Barbera, G., F. Carimi, and P. Inglese. 1993a. Influenza dell'epoca di impianto e del tipo di talea sulla radicazione e sullo sviluppo di barbatelle di *Opuntia ficus-indica* Mill. *Frutticoltura* 10: 67–71.

Barbera, G., F. Carimi, and P. Inglese. 1993b. Effects of GA_3 and shading on return bloom of prickly pear (*Opuntia ficus-indica* (L.) Mill.). *Journal of the South African Society for Horticultural Science* 3: 9–10.

Barbera, G., P. Inglese, and T. La Mantia. 1994. Influence of seed content on some characteristics of the fruit of cactus pear (*Opuntia ficus-indica* Mill.). *Scientia Horticulturae* 58: 161–165.

Basile, F. 1996. *Economia della Produzione e del Mercato dei Fichidindia in Italia.* Università degli Studi, Catania, Italy.

Basile, F., and V. T. Foti. 1997. Economic features of cactus pear production in Italy. *Acta Horticulturae* 438: 139–150.

Battaglia, G. 1997. A study of consumers of cactus pear in the catering industry in central and northern Italy. *Acta Horticulturae* 438: 171–180.

Bazin, R. 1979. *Viaggio in Sicilia.* Edizioni Ristampe Siciliane, Palermo.

Berger, H. S., X. R. Ortuzar, C. M. Auda, M. Lizana, and A. P. Reszczynski. 1978. Conservacion de tunas (*Opuntia ficus-indica*) en almacenaje refrigerado. *Investigacíon Agricóla* (Chile) 4: 21–24.

Bowers, J. E. 1996. Growth rate and life span of a prickly pear cactus *Opuntia engelmannii* in the northern Sonoran Desert. *Southwestern Naturalist* 41: 315–318.

Brutsch, M. O. 1979. The prickly pear (*Opuntia ficus-indica*) as a potential fruit crop for the drier regions of Ciskey. *Crop Production* 8: 131–137.

Brutsch, M. O. 1992 Crop manipulation in spineless prickly pear (*Opuntia ficus-indica*) in South Africa. *Actas II Congreso Internacional de la Tuna y Cochinilla.* Universidad de Chile, Santiago. Pp. 40–47.

Brutsch, M. O. 1997. Climatic data of selected cactus pear *Opuntia ficus-indica* (L.) Mill. growing areas in South Africa. *Acta Horticulturae* 438: 13–20.

Brutsch, M. O., and M. B. Scott. 1991. Extending the fruiting season of spineless prickly pear (*Opuntia ficus-indica*). *Journal of the South African Society for Horticultural Science* 1: 73–76.

Brutsch, M. O., and H. G. Zimmermann. 1993. The prickly pear (*Opuntia ficus-indica* Cactaceae) in South Africa: Utilization of the naturalised weed, and of the cultivated plants. *Economic Botany* 47: 154–162.

Bunch, R. 1996. Cactus pear products at D'Arrigo Bros. *Journal of Professional Association for Cactus Development* 1: 100–102.

Cabras, P., M. Schirra, V. L. Garau, and A. Angioni. 1999. Factors affecting imazalil and thiabendazole uptake and persistence in oranges following dip treatments. *Journal of Agricultural Food Chemistry* 47: 3352–3354.

Cantwell, M. 1995. Postharvest management of fruits and vegetable stems. In *Agroecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 120–136.

Castillo-Castillo, M., and E. Pimienta-Barrios. 1990. Commercialización. *El Nopal: su Conoscimiento y Aprovechamiento.* Universidad Autónoma Agraria Antonio Narro, Saltillo, Mexico. Pp. 336–343.

Chávez-Franco, S., and C. Saucedo-Veloz. 1985. Conservación en refrigeración de los variedades de tunas. *Horticultura Mexicana* 1: 6–13.

Chessa, I., and M. Schirra. 1990. Prickly pear cv. 'Gialla': intermittent and constant refrigeration trials. *Abstracts, XXIII International Horticultural Congress,* Florence. P. 689.

Chessa, I., and G. Barbera. 1984. Indagine sulla frigoconservazione dei frutti della cv. Gialla di ficodindia. *Frutticoltura* 46: 57–61.

Chessa, I., Q. A. Cossu, and S. D'Aquino. 1992. Surface characteristics of prickly pear *(Opuntia ficus-indica* Mill.) fruit during development. In *Proceedings II Congreso Internacional de Tuna y Cochinilla.* Santiago, Chile. Pp. 86–92.

Cicala, A., A. Fabbri, A. Di Grazia, A. Tamburino, and C. Valenti. 1997. Plant shading and flower induction in *Opuntia ficus-indica* (L.) Mill. *Acta Horticulturae* 438: 57–64.

Claassens A. S., and A. B. Wessels. 1997. The fertilizer requirements of cactus pear (*Opuntia ficus-indica* (L.) Mill.) under summer rainfall conditions in South Africa. *Acta Horticulturae* 438: 73–76.

Cohen, E., B. Shapiro, Y. Shalom, and J. D. Klein. 1994. Water loss: A non destructive indicator of enhanced

cell membrane permeability of chilling-injured *Citrus* fruit. *Journal of the American Society for Horticultural Science* 110: 983–986.

Curtis, J. R. 1977. The development of commercial prickly pear farming in the Santa Clara Valley, California. *Cactus and Succulent Journal (U.S.)* 47: 35–37.

Damigella, P. 1958. Una nuova varietà di *Opuntia amyclaea* Tenore (*O. amyclaea* var. *leucosarca*). *Bolettino Istituto Botanica Università di Catania* 1: 34–45.

D'hallewin, G., M. Schirra, and E. Manueddu. 1999. Effects of heat on epicuticular wax of cactus pear fruit. *Tropical Science* 39: 1–4.

Fabbri, A., A. Cicala, and A. Tamburino. 1996. Anatomy of adventitious root formation in *Opuntia ficus-indica* cladodes. *Journal of Horticultural Science* 71: 235–242.

Flores Valdez, C., J. M. Esquivel, and P. Ramirez Moreno. 1995. *Mercato Mundial de la Tuna.* Universidad Autónoma, Chapingo, Mexico.

Garcia de Cortázar, V., and P. S. Nobel. 1992. Biomass and fruit production for the prickly pear cactus, *Opuntia ficus-indica. Journal of the American Society for Horticultural Science* 117: 558–562.

Gathaara, G. N., P. Felker, and M. Land. 1989. Influence of nitrogen and phosphorus on *Opuntia engelmannii* tissue N and P concentrations, biomass production and fruit yield. *Journal of Arid Environments* 16: 337–346.

Gil, G., and A. R. Espinosa. 1980. Fruit development in the prickly pear cactus (*Opuntia ficus-indica* Mill.) with preanthesis application of gibberellin and auxin. *Ciencia Investigacion Agraria* 7: 141–147.

Gorini, F., A. Testoni, R. Cazzola, F. Lovati, M. G. Bianco, I. Chessa, M. Schirra, M. Budroni, and G. Barbera. 1993. Aspetti tecnologici: Conservazione e qualità di fico d'india e avocado. *Informatore Agrario* XLIX 1: 89–92.

Inglese, P. 1994. *Biologia Fiorale e di Fruttificazione* dell'*O. ficus-indica* Mill. *Atti Accademia Nazionale Scienze Lettere ed Arti di Palermo,* Palermo.

Inglese, P., and L. S. Pace. 1999. Contenuto in elementi minerali e fertilità dei cladodi di *O. ficus-indica* Mill. *Atti Convegno "Fruttiferi Tropicali e Subtropicali in Italia.* Ragusa, Italy. Pp. 91–92.

Inglese, P., G. Barbera, and F. Carimi. 1994a. The effect of different amounts of cladode removal on reflowering of cactus pear (*Opuntia ficus-indica* (L.) Miller). *Journal of American Horticultural Science* 69: 61–65.

Inglese, P., A. I. Israel, and P. S. Nobel. 1994b. Growth and CO_2 uptake for cladodes and fruit of the Crassulacean acid metabolism species *Opuntia ficus-indica* during fruit development. *Physiologia Plantarum* 91: 708–714.

Inglese, P., G. Barbera, and T. La Mantia. 1995a. Research strategies for the improvement of cactus pear (*Opuntia ficus-indica*) fruit quality and production. *Journal of Arid Environments* 29: 455–468.

Inglese, P., G. Barbera, T. La Mantia, and S. Portolano. 1995b. Crop production, growth and ultimate size of cactus pear fruits following fruit thinning. *HortScience* 30: 227–230.

Inglese, P., V. Branca, and L. S. Pace. 1996. Influenza della costrizione radicale sullo sviluppo della parte aerea e sulla distribuzione della sostanza secca e dei carboidrati in *Opuntia ficus-indica. Atti III Giornate Scientifiche Società Orticola Italiana.* Erice, Italy. Pp. 83–84.

Inglese, P., T. La Mantia., and G. Barbera. 1998a. Alternanza di produzione e potatura estiva nel ficodindia (*Opuntia ficus-indica* L. Mill.). *Atti IV Giornate Scientifiche Società Orticola Italiana.* San Remo, Italy. Pp. 485–486.

Inglese, P., T. La Mantia, I. Chessa, and G. Nieddu. 1998b. Evolution of endogenous gibberellins at different stages of flowering in relation to return bloom of cactus pear (*Opuntia ficus-indica* L. Mill.). *Scientia Horticulture* 73: 45–51.

Inglese, P., B. Barbera., and T. La Mantia. 1999. Seasonal reproductive and vegetative growth patterns, and resource allocation during cactus pear *Opuntia ficus-indica* (L.) Mill. fruit growth. *HortScience* 34: 69–72.

Kader, A. A. 1999. Produce facts: Cactus (prickly) pear. *Perishable Handling Quarterly Issue* 100: 15–16.

Karim, M. R., Felker, P., and Bingham, R. L. 1998. Correlations between cactus pear (*Opuntia* spp.) cladode nutrient concentrations and fruit yield and quality. *Annals of Arid Zones* 37: 159–171.

Kuty, J. O. 1992. Growth and compositional changes during the development of prickly pear fruit. *Journal of Horticultural Science* 67: 861–868.

Lakshminarayana, S., L. Alvarado, and F. Perez. 1979. The development and postharvest physiology of the fruit of prickly pear (*Opuntia amyclaea* Tenore). *Tropical Food* 1: 69–93.

Lakshminarayana, S., and I. B. Estrella. 1978. Postharvest respiratory behaviour of tuna (prickly pear) fruit (*Opuntia robusta* Mill.). *Journal of Horitcultural Science* 53: 327–330.

La Mantia, T., G. Barbera., and P. Inglese. 1997. Effect of shading on growth and ripening of fruits of cactus pear (*Opuntia ficus-indica* L. Miller). *Journal of Horticultural Science* 72: 299–304.

La Mantia, T., G. Barbera, G. Gugliuzza, and P. Inglese. 1998. Interazione tra irrigazione ed entità di fruttificazione e qualità dei frutti di ficodindia (*O. ficus-indica* (L.) Mill.). *Atti Giornate Scientifiche SOI.* San Remo, Italy. Pp. 241–242.

Luo, Y., and P. S. Nobel. 1993. Growth characteristics of newly initiated cladodes of *Opuntia ficus-indica* as affected by shading, drought and elevated CO_2. *Physiologia Plantarum* 87: 467–474.

Lurie, S. 1998. Postharvest heat treatments of horticultural crops. *Horticultural Reviews* 22: 91–121.

Mazzola, P., S. Romano, and P. Fici. 1988. Contributo alla conoscenza del genere *Opuntia* Miller. I dati cariologici e distributivi delle specie spontaneizzate coltivate in Sicilia. *Naturalista Siciliano IV* 12: 159–168.

Mondragon-Jacobo, C., and E. Pimienta-Barrios. 1995. Propagation. In *Agroecology, Cultivation and Uses of Cactus Pear* (G. Barbera., P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 64–70.

Monselise, S. P., and R. Goren. 1987. Preharvest growing conditions and postharvest behavior of subtropical and temperature-zone fruits. *HortScience* 22: 1185–1189.

Monjauze, A., and H. B. Le Houerou. 1965. Le role des *Opuntia* dansl'economie agricole Nord Africaine. *Extrait du Bulletin de l'École Nationale Superieure d'Agriculture de Tunis* 8–9: 85–164.

Moreno-Rivera, M. A., L. Alvarado-Sosa, and S. Lakshminarayana. 1979. Preharvest respiratory trend of the fruit of prickly pear (*Opuntia amyclaea* T.). *Proceedings Journal of Florida State Horticultural Society* 92: 235–237.

Mulas, M., and G. D'hallewin. 1990. Improvement pruning effects on vegetative and yielding behaviour in prickly pear (*Opuntia ficus-indica* Mill.) "Gialla" cultivar. *Acta Horticulturae* 296: 139–146.

Mulas, M., and G. D'hallewin. 1997. Fruit quality of four cactus pear (*Opuntia ficus-indica* Mill.) cultivars as influenced by irrigation. *Acta Horticulturae* 438: 115–122.

Nerd, A., and Y. Mizrahi. 1993. Modern cultivation of prickly pear in Israel: fertigation. *Acta Horticulturae* 349: 235–237.

Nerd, A., and Y. Mizrahi. 1997. Reproductive biology of cacti. *Horticultural Review* 18: 321–346.

Nerd, A., and P. S. Nobel. 1995. Accumulation, partitioning, and assimilation of nitrate in *Opuntia ficus-indica. Journal of Plant Nutrition* 18: 2533–2549.

Nerd, A., A. Karady, and Y. Mizrahi. 1989. Irrigation, fertilization, and polyethylene cover influence bud development in prickly pear. *HortScience* 24: 773–775.

Nerd, A., A. Karady, and Y. Mizrahi. 1991. Out-of-season prickly pear: Fruit characteristics and effect of fertilization and short droughts on productivity. *HortScience* 26:527–529.

Nerd, A., R. Mesika, and Y. Mizrahi. 1993. Effect of N fertilizer on the autumn floral flush and cladode N in prickly pear *Opuntia ficus-indica* (L.) Mill. *Journal of Horticultural Science* 68: 337–342.

Nieddu, G., and D. Spano. 1992. Flowering and fruit growth in *Opuntia ficus-indica. Acta Horticulturae* 296: 153–159.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nobel, P. S., and M. Castañeda. 1998. Seasonal, light and temperature influences on organ initiation for unrooted cladodes of the prickly pear cactus *Opuntia ficus-indica. Journal of the American Society for Horticultural Science* 123: 47–51.

Nobel, P. S., C. E. Russell, P. Felker, M. Galo, and E. Acuna. 1987. Nutrient relations and productivity of prickly pear cacti. *Agronomy Journal* 79: 550–555.

Ochoa, J. 1997. Estado actual del nopal en la Republica Argentina. *VII Congreso sobre Conocimiento y Aprovechamento del Nopal,* Monterrey, Mexico. Pp. 15–19.

Parish, J., and P. Felker. 1997. Fruit quality and production of cactus pear (*Opuntia* spp.) fruit clones selected for increased frost hardiness. *Journal of Arid Environments* 37: 123–143.

Piga, A., S. D'aquino, M. Agabbio, and M. Schirra. 1996. Storage life and quality attributes of cactus pears cv. 'Gialla' as affected by packaging. *Agricoltura Mediterranea* 126: 423–427.

Piga, A., G. D'hallewin, S. D'Aquino, and M. Agabbio. 1997. Influence of film wrapping and UV irradiation on cactus pear quality after storage. *Packaging Technology and Science* 10: 59–68.

Pimienta-Barrios, E. 1990. *El Nopal Tunero.* Grafica Nueva, Pipila 638. Guadalajara, Mexico.

Pimienta-Barrios, E., and A. Munoz-Urias. 1995. Domesti-

cation of Opuntias and cultivated varieties. In *Agroecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, E. Pimienta-Barrios, eds). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 58–63.

Pimienta-Barrios, E., Q. Loera, and L. O. Lopez. 1992. Estudio anatomico comparativo en morfospecies del subgenero opuntia. *Actas III Congreso Internacional de Tuna y Cochinilla.* Santiago, Chile. Pp. 30–39.

Pimienta-Barrios, E., G. Barbera, and P. Inglese. 1993. Cactus pear (*Opuntia* spp. Cactaceae) International Network: an effort for productivity and environmental conservation for arid and semiarid lands. *Cactus and Succulent Journal* (*U.S.*) 65: 225–229.

Potgieter, J. P., and J. J. Mkhari. 2000. Effects of N, P, K and lime application on cactus pear (*Opuntia* spp.) fruit yield and quality under rainfed conditions in South Africa. *Abstracts, IVth International Congress on Cactus Pear and Cochineal,* Hammamet, Tunisia. P. 37.

Rodriguez-Felix, A., M. I. Gonzalez-Salas, H. Soto-Valdez, and I. Silveira-Gramont. 1992. Effects of postharvest treatments on the quality of tuna during storage. *Proceedings of the 3rd Annual Texas Prickly Pear Council,* Kingsville, Texas. Pp. 9–21.

Saenz Hernandez, C. 1985. La tuna (*Opuntia ficus-indica*): Un cultivo con perspectivas. *Alimentos* 3: 47–49.

Schirra, M., G. D'hallewin, P. Inglese, and T. La Mantia. 1999a. Epicuticular changes and storage potential of cactus pear (*Opuntia ficus-indica* Miller (L.)) fruit following gibberellic acid preharvest sprays and postharvest heat treatment. *Postharvest Biology and Technology* 17: 79–88.

Schirra, M., P. Inglese, and T. La Mantia. 1999b. Quality of cactus pear (*Opuntia ficus-indica* Miller (L.)) fruits in relation to ripening time, $CaCl_2$ preharvest sprays and storage conditions. *Scientia Horticulturae* 1362: 1–12.

Schirra, M., M. Agabbio, S. D'Aquino, and T. G. McCollum. 1997a. Postharvest heat conditioning effects on early ripening 'Gialla' cactus pear fruit. *HortScience* 36: 159–165.

Schirra, M., G. Barbera, G. D'hallewin, P. Inglese, and T. La Mantia. 1997b. Response of cactus pear fruit to $CaCl_2$ preharvest treatments and prestorage heat conditioning. *Journal of Horticultural Science* 72: 371–377.

Schirra, M., G. Barbera, S. D'Aquino, T. La Mantia, and R. E. McDonald. 1996. Hot dips and high temperature conditioning to improve shelf quality of late-crop cactus pear fruit (*Opuntia ficus-indica* L. Mill.). *Tropical Science* 36: 159–165.

Sudzuki, F., C. Munoz, and H. Berger. 1993. *El Cultivo de la Tuna* (*Cactus Pear*). Universidad de Chile, Santiago.

Testoni, A., and P. Eccher Zerbini. 1990. Conservazione del fico d'india in atmosfera normale e controllata. *Annali Istituto Valorizzazione Tecnologica Prodotti Agricoli* XXI, Milan. Pp. 131–137.

Van Der Merwe, L. L., A. B. Wessels, and D. I Ferreira. 1997. Supplementary irrigation for spineless cactus pear. *Acta Horticulturae* 438: 77–82.

Weiss, J., A. Nerd, and Y. Mizrahi. 1993. Vegetative parthenocarpy in the cactus pear *Opuntia ficus-indica* (L.) Mill. *Annals of Botany* 72: 521–526.

Wessels, A. B. 1988. *Spineless Prickly Pear.* First Perskor Publishers, Johannesburg.

Wessels, A. B., L. L. Van Der Merwe, and H. Du Plessis. 1997. Yield variation in clonally propagated *Opuntia ficus-indica* (L.) Mill. plants when terminal cladodes are used. *Acta Horticulturae* 438: 73–76.

CHAPTER

› 11 ‹

FRUITS OF VINE AND COLUMNAR CACTI

Avinoam Nerd, Noemi Tel-Zur, and Yosef Mizrahi

Introduction
Vine Cacti
Cytology
Pollination
Environmental Constraints
Fruit Properties
Columnar Cacti
Stenocereus queretaroensis
Other Stenocereus *Species*
Cereus peruvianus
Vine and Columnar Cacti as World Fruit Crops
Hylocereus
Selenicereus megalanthus
Stenocereus *and* Cereus
Conclusions and Future Prospects
Literature Cited

Introduction

Medium to large edible cactus fruits are produced by members of subfamily Cactoidae, tribe Cacteae. They are known in Latin America as pitahaya or pitaya: pitahaya generally refers to fruits of vine (climbing) species and pitaya to fruits of columnar (erect) ones, although considerable variation exists (Ortiz 1999). Unlike the widely cultivated cactus pear (*Opuntia ficus-indica,* subfamily Opuntioideae; Chapter 10), pitayas and pitahayas have small digestible seeds and lack the barbed small spines (glochids) that cause difficulties in the handling of cactus pear. Their peel is either spineless or spiny, but the spines usually are large and easily removed upon ripening. Since 1980, an effort has been made to cultivate vine cacti in genera *Hylocereus* and *Selenicereus* and columnar cacti in genera *Cereus* and *Stenocereus* (Table 11.1, which includes common names of ethnic origin or created by growers). *Hylocereus undatus* is the most popular vine cactus and is a worldwide crop (Table 11.1). Among the columnar cacti, *Stenocereus queretaroensis* is the most cultivated, although the growth area is restricted to central Mexico. Research on pitahaya and pitaya crops is in its infancy. This chapter considers the identity, environmental limits, horticultural aspects, and commercialization of the main cultivated species.

TABLE 11.1
Vine and columnar cacti cultivated for their fruits

Species	Common names	Main cultivation countries	Fruit characteristics
Vine cacti			
Hylocereus costaricensis (Weber) Britton & Rose	Pitahaya, pitahaya roja, red pitahaya	Nicaragua, Guatemala	Large globose; peel dark red (rarely yellow) with large scales; pulp deep red
H. polyrhizus (Weber) Britton & Rose	Pitahaya, pitahaya roja, red pitahaya, red Eden (Israel)	Israel	Large oblong; peel dark red with large scales; pulp violet-red
H. undatus (Haworth) Britton & Rose	Pitahaya, pitahaya roja, red pitahaya, dragon fruit (Asia), Eden (Israel)	Vietnam, Mexico, Taiwan, Thailand, Cambodia, Israel, Philippines	Large oblong; peel red (rarely yellow) with large greenish scales; pulp white
Selenicereus megalanthus (Schun ex Vampel) Moran *(Mediocactus coccineus, M. megalanthus)*	Pitahaya, pitaya amarilla, yellow pitaya	Colombia, Ecuador, Israel	Medium oblong; peel yellow with tubercles and spines; pulp white
Columnar cacti			
Cereus peruvianus (L.) Miller (*C. jamacaru, C. uruguayanus*)	Pitaya, apple cactus, Koubo (Israel)	Israel, United States (California)	Medium-large oblong; peel smooth, spineless, usually red; pulp white
Stenocereus griseus (Haworth) Buxbaum	Pitaya, pitayo de Mayo	Mexico	Green or red skin; pulp reddish
S. queretaroensis (Weber) *Buxbaum*	Pitaya, pitaya de Queretaro	Mexico	Medium globose; peel with spines, green or red; pulp white or colored, often purple
S. stellatus (Pfeiffier) Riccobobo	Pitaya, pitaya de Augusto	Mexico	Medium globose; peel with spines, green or red; pulp white or colored

Vine Cacti

Cytology

Chromosomes in the Cactaceae have a base number of n = 11 (Gibson and Nobel 1986). Cultivated *Hylocereus* species (*H. costaricensis, H. polyrhizus,* and *H. undatus*) and most investigated *Selenicereus* species are diploids ($2n$ = 22), although the highly cultivated *S. megalanthus* (syn. *Mediocactus megalanthus* or *M. coccineus;* Moran 1953; Infante 1992; Weiss et al. 1995) is tetraploid ($2n$ = 44; Beard 1937; Spencer 1955; Lichtenzveig et al. 2000). *Selenicereus megalanthus* has morphological features of both *Hylocereus* and other *Selenicereus* species (Britton and Rose 1963) and is cross-compatible with several *Hylocereus* spp., suggesting that *S. megalanthus* originated from an intergeneric hybridization between species of *Hylocereus* and *Selenicereus* (Lichtenzveig et al. 2000).

No major barriers seem to limit interspecific crossing among *Hylocereus* spp. Fruits obtained by such crossings are large, and the majority of the seeds germinate (Weiss et al. 1994b). Their hybrids show a normal meiosis, with 11 bivalents at metaphase I, and produce pollen of high viability and seeds with high germination rates (Lichtenzveig et al. 2000). Pollen viability for *S. megalanthus* is significantly lower than that for *Hylocereus* spp. and is associated with the pairing of multivalents and consequently the occurrence of univalents at metaphase I, which leads to pollen or ovules with chromosomal disorders (Lichtenzveig et al. 2000). *Selenicereus megalanthus* crossed with *Hylocereus* hybrids are triploids, aneuploids, or polyploids with different chromosome numbers (N. Tel-Zur, S. Abbo, and Y. Mizrahi, unpublished observations). The ability to produce hybrids by interspecific and intergeneric crosses is utilized in Israel for breeding cultivars with desired fruit characteristics (such as improved taste) or greater environmental flexibility. Modern molecular techniques (Chapter 15) may elucidate the genetic relationship among vine cacti underlying such features. An effective procedure has been

developed for DNA extraction from *Hylocereus* and *Selenicereus* (Tel-Zur et al. 1999).

Pollination

Studies of breeding systems conducted in Israel (Weiss et al. 1994a; Nerd and Mizrahi 1997; Lichtenzveig 2000) show that *Hylocereus* spp. are self or partially incompatible, and foreign pollen (pollen of other *Hylocereus* spp.) is required for fruit set. *Selenicereus megalanthus* is self-compatible, as fruit can set with its own pollen. However, in certain clones larger fruit are obtained using pollen of other *S. megalanthus* clones, indicating partial self-incompatibility (Lichtenzveig et al. 2000). Climate conditions can also affect compatibility; at the end of the warm Israeli summer, high temperatures decrease *H. undatus* fruit set with self pollen. Natural pollinators of vine cacti seem to be bats and hawkmoths (Nerd and Mizrahi 1997). In orchards of vine cacti planted in the tropics, pollination is achieved without human intervention. In Israel, pollination is done by hand due to a lack of pollen vectors (Weiss et al. 1994a). Pollen preservation (Metz et al. 2000) allows for cross-pollination for times when there is no synchronization between the flowering of different *Hylocereus* crops.

Environmental Constraints

Vine cacti are native to tropical regions of North and South America, using their triangular slender stems, equipped with adventitious roots, to spread on trees. They are successfully cultivated outdoors in cloudy tropical regions (Central America and the Far East); e.g., *H. undatus* grows successfully in southern Vietnam and Taiwan without any shading (Fig. 11.1A). However, in Israel, where solar radiation is high (noon photosynthetic flux densities can reach 2,200 μmol m^{-2} s^{-1} in the summer), plants exposed to full sunlight can bleach, degenerate, and produce low quality fruit with poor color and low sugar concentrations (Raveh et al. 1997, 1998; Mizrahi et al. 1997; Mizrahi and Nerd 1999). Hence, plants are maintained under shade nets (Fig. 11.1B). Certain species, such as *H. costaricensis* and *H. polyrhizus,* have a higher light tolerance, probably due to their waxy thick skin that reduces the transmittance of light to the inner tissues of the stem. Orchards for such species in Israel are established in net houses with shading ranging from 20 to 60%—the higher shading being used in warmer regions (Mizrahi and Nerd 1999). The intensity of solar radiation changes during the daytime and depends on season, so control of light should be considered. Plants of *Hylocereus* spp. exposed to full sunlight in the spring have early blooming and early seasonal fruit production.

Vine cacti are sensitive to chilling temperatures and the stems bleach when night temperatures decline below about 5°C. Severe injuries appear when air temperatures approach zero; round yellow lesions develop along the stems and stem segments die. Subfreezing temperatures (−3°C) kill most of the collected germplasm in Beer-Sheva, Israel (Mizrahi and Nerd 1999). Observations in Beer-Sheva show significant differences among species in cold tolerance, as frost events totally damage *Hylocereus* sp. #10487 (unidentified species cultivated in Israel) and *Selenicereus megalanthus,* moderately damage *H. undatus,* and slightly damage *H. costaricensis* and *H. polyrhizus.* Plants recover easily when temperatures rise, but yields are reduced. In areas with cold temperatures, plastic coverings or glasshouses are recommended (Mizrahi and Nerd 1999).

In Israel water and fertilizer are commonly applied by drip irrigation almost year-round, except in the rainy periods (Nerd and Mizrahi 1998; Nerd et al. 1999). Vegetative growth and fruit production in the hot internal valleys (Jordan and Arava) occur later than in the more moderate coastal region. A well-developed canopy (1.8 m high in rows that are 2.5 m apart) is obtained for *H. undatus* at the 3rd year in the coast region, whereas 5 to 6 years is required in the valleys; annual fruit yield of the full canopy orchard is 32 to 40 tons ha^{-1} at the coast versus 2 to 3 tons ha^{-1} in the warmer and drier valleys. Because the rates of fruit-set and the average fruit weight are similar for the valleys and the coast, the small number of flowers produced in the valleys is likely the predominate factor in the low yields. The high summer temperatures (monthly maximum/minimum air temperatures are 38/25°C, 7 to 10°C higher than those at the coast) or the saline irrigation water in some locations (electrical conductivity of soil water = 3–4 decisiemens m^{-1} at Arava versus 1 dS m^{-1} near the coast) probably inhibits flower induction. High summer temperatures in the valleys cause daily net CO_2 uptake to be small or negative for vine cacti (Raveh et al. 1995), so deficiency of photosynthate can also explain the slow growth rate and low fruiting in the valleys.

In response to high air temperatures (43–46°C) that occur during warm summers in Israel, stems can turn brown and become liquefied (Fig. 11.1B). *Hylocereus undatus* is the most sensitive of the cultivated vine cacti; in the summer of 1998 in the Arava Valley, about 50% of its total stem length was damaged versus less than 10% for *H. costaricensis* and *H. polyrhizus,* and none for *S. megalanthus.* Similar results occur for a germplasm collection that is located in a greenhouse in Beer-Sheva under unusual extreme summer temperatures (Mizrahi and Nerd 1999). Shade reduces the heat damage.



Figure 11.1. (A) *Hylocereus undatus* on single-plant trellis system in Taiwan and (B) *H. undatus* (on left) and *Hylocereus polyrhizus* (on right) on row trellis system under shade net (shade cloth) in Israel, where injury occurred on *H. undatus* at high summer temperatures of 45°C.

Fruit Properties

Fruits of vine cacti are medium-sized to large berries with a thin, colored peel and white or colored, juicy pulp (Table 11.1) containing numerous small, soft, digestible seeds. The peels of *Hylocereus* spp. have scales that contribute to the attractive appearance of the fruits, which also are used decoratively. For *Selenicereus megalanthus,* the peel is covered with spiny tubercules, but the spines are readily shed upon ripening. Fruits of *Hylocereus* crops are usually large (up to 1,000 g), two- to threefold heavier than those of *S. megalanthus.*

Studies in Israel (Weiss et al. 1994b; Nerd and Mizrahi 1998, 1999; Nerd et al. 1999) show that fruit growth for *H. costaricensis, H. polyrhizus, H. undatus,* and *S. megalanthus* follows a sigmoid pattern, with a low or negligible growth rate during the last phase when ripening occurs. A change in peel color (color-break) indicates the beginning of the last phase. For *H. polyrhizus,* which has a red-violet pulp, the accumulation of pulp pigments occurs in parallel with the development of peel color. During the last phase, pulp content (as a percentage of fruit fresh weight) increases markedly (from 20–30% at the beginning to 60–80% at the end of the phase), pulp titratable acidity declines, and pulp contents of soluble sugars and soluble solids increase (reaching maximal levels of 7–9% and 14–18%, respectively, of the fresh weight at full color). Degradation of starch, which increases in the pulp prior to ripening, accounts partially for the accumulation of soluble sugars. For *H. undatus,* amylase and invertase activity is correlated with the increase in pulp soluble sugars (mainly fructose and glucose), which reach their highest concentrations at the center of the pulp (Wu and Chen 1997). The fruits are classified as nonclimacteric, reflecting the low production rates of CO_2 and ethylene during ripening (Nerd and Mizrahi 1998; Nerd et al. 1999).

Palatability tests on fruits picked at different ripening stages (determined according to the number of days after anthesis or the appearance of peel color) indicate that fruits are most palatable at advanced ripening stages or at full color. Similar to many other fleshy fruits, growers tend to harvest the fruits of vine cacti prior to full ripeness when the peel is still mostly green in order to prolong the marketing life of the fruit (Barbeaue 1990; Cacioppo 1990). However, ripening of such fruits is not as good compared with those left to ripen on the vine. For example, fruits of *S. megalanthus* picked at color-break and held at 10 to 20°C attain the physical appearance of fruits ripened on the plant and their acidity decreases, but the soluble sugars remain low and the flavor is poor (Nerd and Mizrahi 1999). Hence, the optimum stage for harvesting fruits of vine cacti for high consumption quality under usual storage conditions should be at close to full ripeness, as evidenced by almost full or full color development.

The shelf life of fruits of *Hylocereus* species is about 7 to 10 days at room temperature (about 20°C; Nerd et al. 1999). Shelf life is limited by senescence symptoms, such as a sharp decline in acidity and sugars, scale yellowing and shriveling, and fruit softening. Fruits can be stored for 14 days at 10 to 12°C and longer under lower temperatures (4–6°C), but upon transfer to room temperature they tend to develop chilling injury symptoms, such as peel browning and decay. Similarly, fruits of *S. megalanthus* are sensitive to chilling temperatures, but the storage life (at 10–12°C) is at least twice as long as for *Hylocereus* fruits (Nerd and Mizrahi 1999).

Vine cacti produce several floral flushes during the flowering season, and predicting the harvest time is important for orchard management and fruit marketing (Mizrahi and Nerd 1999). Little is known about the effect of plant and environmental factors on the duration of fruit growth for vine cacti, but temperature appears to be a dominant factor. In Israel *Hylocereus* spp. produces three or four flushes during the warm season (June–October); 30 to 35 days elapse from anthesis to full fruit color when daily temperatures average 25°C, but 40 to 45 days are required when daily temperatures average 20°C (Nerd et al. 1999). Flowering of *S. megalanthus* in Israel occurs mainly in the autumn, when air temperatures decrease and the duration of fruit development is much longer than for *Hylocereus* spp. The increased development time is due to the lower temperatures during fruit growth and the lower inherent growth rate for the fruit of *S. megalanthus* (Nerd and Mizrahi 1998). The time from anthesis to full ripening for *S. megalanthus* varies from 120 days (average daily temperatures of 25°C) to 180 days (20°C). The positive correlation between air temperature and fruit growth enables the development of a heat-unit model to predict the period from anthesis to maturity for *S. megalanthus* (Nerd and Mizrahi 1998).

Columnar Cacti

Columnar cacti are much less cultivated for fruit than are vine cacti, and little is known about their environmental flexibility (Mizrahi et al. 1997). Among them, *Stenocereus* spp. are the most cultivated. They are planted in Mexico in or near their natural habitats, which have a semitropical climate with both summer (about 65%) and winter rains for a total of 400 to 800 mm annually (Pimienta-Barrios and Nobel 1994; Pimienta-Barrios et al. 1997). Monthly av-

erages of daily air temperatures range from 8 to 18°C at night and from 24 to 34°C during the daytime. Temperature fluctuations from the coldest to the warmest month is only 8°C at any particular site. Each species will be considered separately.

Stenocereus queretaroensis

Stenocereus queretaroensis is probably the commercially most important species of the genus (Pimienta-Barrios and Nobel 1994). It is also the most investigated (Nobel and Pimienta-Barrios 1995; Pimienta-Barrios et al. 1997; Pimienta-Barrios 1999). Fruits reach the local markets from three sources: (1) wild stands, (2) wild stands enriched with cuttings of selected clones (managed *in situ*), and (3) cultivated selected clones established from cuttings in home gardens and small plantations (Fig. 11.2). Many commercially productive stands come from relict ones, namely those associated with archeological sites dating back as long as 2,300 years BP (Benz et al. 1997). Today's plants are offspring from ancestors selected in pre-Columbian times, with better horticultural features having evidently gone through selection by humans for many years (Benz et al. 1997).



Figure 11.2. Orchard of *Stenocereus queretaroensis* in southwestern Jalisco, Mexico. Photograph courtesy of Park S. Nobel.

Fruit weights of *S. queretaroensis* average 100 to 200 g. The pulp is very tasty, has different colors according to the clone (white, pink, orange, red of various hues, and purple), and contains soft edible small seeds. The spines are soft, abscise upon ripening, and can easily be removed by hand. The best clones are found in relict stands near archeoligical sites, and fruit productivity per plant correlates with the canopy width, probably due to length of the branches on which the fruits are produced. Annual production of 100 fruits per plant yields about 17 tons fresh weight ha^{-1} $year^{-1}$ from the best orchards (Benz et al. 1997). The best-known clone is 'Mamey,' whose fruit can reach the size of 165 g fresh weight. The peel is 18 to 24% of the fruit fresh weight under cultivation, which is better (lower) than for the much more common cactus pear, whose peel is about 45% of the fruit fresh weight (Pimienta-Barrios et al. 1997). The fruit shelf life is only a few days, partly because the fruits split (dehisce) and the pulp is exposed to contamination by bacteria and fungi. This very short shelf life, even for non-splitting fruit, is the main constraint on its commercialization (Pimienta-Barrios et al. 1997). In spite of this shortcoming, workers involved with this fruit earn the same to three times as much as other wage earners in the region (Benz et al. 1997). Another important factor that limits the domestication of *S. queretaroensis* is its relatively low growth rate. Ten years are required for an orchard to obtain large enough fruit production to reach profitability. On the other hand, 100 years of production are expected from this plant, reaching its peak at 40 years of age (Pimienta-Barrios et al. 1997). This pitaya does not respond to traditional management, such as irrigation and fertilization, possibly due to symbiotic association with mycorrhizae or genetic inflexibility (Pimienta-Barrios and Nobel 1995; Pimienta-Barrios et al. 1997).

Stenocereus queretaroensis in Mexico flowers in February and March, the beginning of the dry season. Fruits ripen mainly in May and are harvested at the ripe stage. The soluble sugars comprise 10 to 11% of the fruit fresh weight for various cultivars (Pimienta-Barrios et al. 1994, 1997). The fruits are sour (pH 4.5–5.0), with the acid content ranging between 0.15 to 0.5% of the fruit fresh weight. Fruits of *S. queretaroensis* have to be sold immediately because of a very short storage and shelf life, as they readily split open (Pimienta-Barrios and Nobel 1994; Pimienta-Barrios et al. 1997); this, as already indicated, is the main restricting factor in the commercialization of this species.

Other Stenocereus *Species*

Stenocereus stellatus is the commercially second most important columnar cactus in Mexico. Known locally as "xoconochtli," archeological evidence shows that it was consumed by humans as long as 7,000 years BP (Chapter

9). Today *S. stellatus* has the same three major sources of fruits as for *S. queretaroensis* (Casas et al. 1997, 1999a,b). It is grown in semitropical areas with average annual temperatures of 17 to 24°C and annual rainfall of 440 to 760 mm. Fruit weight is less than that of *S. queretaroensis,* ranging from 20 to 80 g; the number of fruits per plant varies from 12 to 187. The maximum density of plants in home gardens is 780 ha^{-1}, and the highest yield is 3.3 tons ha^{-1} $year^{-1}$. Fruits vary in skin color—some are green (preferred in home gardens) and most are red. Pulp color is red in wild ones, whereas under cultivation pink, purple, yellow, orange, and white pulp can also be found. In the wild the taste is usually sour, whereas cultivated fruits are sweet and sometimes insipid. Some fruits are very spiny, but others have few spines. Upon ripening, spines can be easily removed. Locals prefer the less spiny, larger sweet fruits with a green peel and white flesh (Casas et al. 1997, 1999a). Plantations established from cuttings (about 1 m in length) bear abundant fruits during the fourth year, although some fruits may be obtained one year after planting but are followed by no fruits in the second year (Casas et al. 1997). In the Negev Desert of Israel, even under fertigation (irrigation with water plus specific nutrients), *S. stellatus* produces low amounts of small fruits with no promise of being a commercial orchard crop (Nerd et al. 1993). As for many other columnar cacti, this species flowers nocturnally with self-incompatibility. Also, some genotypes cannot pollinate each other, suggesting that S genes are active (Casas et al. 1999b).

Stenocereus griseus is of a more tropical nature than the other cultivated *Stenocereus* species (Silvius 1995). Its common name, Pitaya de Mayo, means ripening in May (Mizrahi et al. 1997). The fruit is relatively large (100–200 g) and of good quality, similar to other *Stenocereus* spp. In Venezuela there are two ripening seasons, May–early June and late August–early September, corresponding to the rainy seasons (Silvius 1995). In Israel when regularly fertigated (Nerd et al. 1993), flowers appear in late April to May and again in July and in October. Fruits occur in late May (hot valleys) and June to August, but no fruits occur from the October flowering, possibly because temperatures at this time will not support fruit growth. It is sensitive to subfreezing temperatures and has a poor tolerance to salinity (Nerd et al. 1993). *Stenocereus griseus* is harvested and marketed only in Mexico (Pimienta-Barrios and Nobel 1994).

Cereus peruvianus

Cereus peruvianus has only recently been domesticated and its origin is obscure, although possibly it comes from Brazil (Mizrahi and Nerd 1999). *Cereus jamacaru* from northeastern Brazil and *C. uruguayanus* from Argentina are closely related species or even the same one (Taylor and Zappi 1992; R. Kiesling, personal communication). The species is common in gardens in tropical and subtropical countries and has been planted commercially on a small scale in Israel. In comparison to various *Stenocereus* spp. examined in Israel, *C. peruvianus* has significantly higher growth and precocious yielding (Nerd et al. 1993). The common commercial trade name given by the Israeli export company AGREXCO is 'Koubu' to distinguish between the fruit of this species and other pitayas (Mizrahi and Nerd 1999).

Growth and fruiting of *C. peruvianus* in Israel are significantly higher near the coast than in the internal warm valleys or the cold Negev Highlands, where frost (air temperatures decline to −7°C) damages the plants (Nerd et al. 1993). The species is sensitive to salinity (electrical conductivity of the irrigation water of 4 dS m^{-1}), particularly when Na and Cl are the predominating ions (Nerd et al. 1993). Israel uses *C. peruvianus* as a fruit crop, but in South Africa it is considered a weed (Moran and Zimmerman 1991). In Brazil it is used for its valuable gum and polysaccharides (Alvarez et al. 1992, 1995), and various vegetative micropropagation techniques have been developed (Deoliveira et al. 1995; Machado and Prioli 1996). *Cereus peruvianus* is self-incompatible and requires cross-pollination to obtain fruits (Weiss et al. 1994a; Silva and Sazima 1995; Nerd and Mizrahi 1997). In spite of its nocturnal flower opening, daytime-active honey bees can act as pollinators using the few hours the flowers are open in the late evening or early morning (Weiss et al. 1994a; Nerd and Mizrahi 1997; Mizrahi and Nerd 1999). However, when large plants produce hundreds of flowers in a wave in Israel, honey bees fail to cross pollinate the flowers efficiently; hand pollination is then needed to obtain high fruit set and large fruits.

Cereus peruvianus during the warm season in Israel produces several flower flushes. Fruit development differs significantly from that of vine cacti, exhibiting a double sigmoid growth curve with an early and a late rapid growth phase and a slow intermediate growth phase (Weiss et al. 1994a; Wang 1997). Color-break designates the beginning of the last phase, and fruits are fully colored at the end of this phase. During the last phase, pulp fresh weight increases significantly, whereas peel fresh weight remains almost constant; for fully developed fruits, the pulp comprises 70 to 80 % of the fruit fresh weight versus 15 to 20% for young fruits. Ripening occurs during the last phase; firmness and acidity decrease and soluble sugars and total soluble solids increase (to 8–10% and 12–13% of pulp fresh



Figure 11.3. Fruits of *H. undatus* packed in Israel for export to Europe.

weight, respectively) at full color (Wang 1997). Similar to vine cacti, the optimum harvest stage is when the fruits are close to or at full ripeness. Fruits of *C. peruvianus* tend to crack during ripening and in certain genotypes black areas appear on the peel when fruits mature or are touched during harvest. The tendency for both disorders is genetically inherited and can be overcome by clonal selection. For *C. peruvianus* in Israel, about 40 days elapse from anthesis to full color when daily temperatures average 28°C versus 42 to 47 days when temperatures average 24°C (Wang 1997). Fruits of *C. peruvianus* are similar to those of *S. megalanthus* with regard to storage and shelf life.

Vine and Columnar Cacti as World Fruit Crops

Hylocereus

The most widely cultivated vine cactus is the red pitahaya, *Hylocereus undatus* (red peel, white pulp; Fig. 11.3). Its utilization as a major commercial fruit crop has its origins in Vietnam (V. Van Vu, personal communication). The plant was introduced to Indochina by the French around 1860, where it is now considered to be a native plant. Orchards in Vietnam are established from selected clones, and the estimated cultivated area in southern Vietnam is 6,000 ha. The fruits produced ("dragon fruit," or *thang loy* in Vietnamese) are common in local markets and are also exported to Asian and European countries. *Hylocereus undatus* is now spreading in many Asian countries, such as Thailand, Laos, Indonesia, Cambodia, Taiwan, and recently Japan (Okinawa), using clones from Vietnam. Horticultural research in Taiwan indicates a strong local interest in the fruit (Feng-Ru and Chung-Ruey 1997a,b). Other vine pitahayas, such as *H. costaricensis* and *S. megalanthus,* were also introduced to Taiwan and are used for both cultivation and breeding. In addition to the fruit, fresh and dry flowers are also consumed in Taiwan as a vegetable. The development of the *H. undatus* industry is also very intensive in Mexico (Ortiz 1999; Canto 2000), and the estimated present planted area there is about 2,000 ha, half of it in the Yucatan peninsula where it can be found in the wild and has been utilized from pre-Columbian times. Most of the crop in Mexico is sold in local markets.

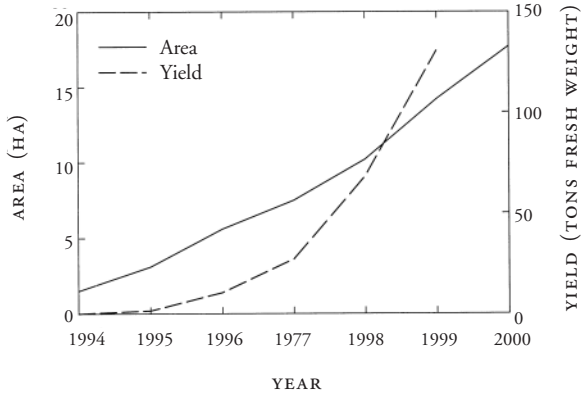


Figure 11.4. Increase in plantation area and fruit yields of vine cacti in Israel during the 1990s.

In Israel the cultivation of *H. undatus* is expanding rapidly, reaching nearly 20 ha in 2000. Export to Europe started in 1996 with 10 tons and in 1999 was about 130 tons (Fig. 11.4). Under the dry climate of Israel, fruit quality is high and most of the harvested crop is marketable. The main difficulties for export are the short storage life of the fruit and the non-stable fruit supply; flowering and harvests occur in waves (Mizrahi and Nerd 1999). Also other countries, such as Australia, New Zealand, the United States (Florida and California), Spain, and the Philippines, are developing the cultivation of *H. undatus.*

Hylocereus costaricensis (red peel, red pulp) is cultivated mainly in Nicaragua, established from clones selected from the wild. The fruits ripen during the rainy season and most of the yield is heavily infested with insects, bacteria, and fungi so that only a small fraction of harvested fruit can be sold as fresh fruit. Export is mainly to Europe under the brand name 'Pitanica.' Today most of the cultivated 6,000 ha are aimed at pulp production, highly demanded by the food industry in the United States and Europe as a natural food ingredient and a colorant (Ortiz 1999; Canto 2000). Guatemala is also producing significant quantities of this fruit, with several other types of red peel/red pulp vine pitahayas. Fruits of *Hylocereus polyrhizus* have a red peel, as for *H. costaricensis,* but have a red-violet pulp. The crop is planted in Israel as a pollinator for *H. undatus.* Usually red vine pitahaya orchards consist of 20% *H. polyrhizus* and 80% *H. undatus.* Because of the sour taste, fruit *H. polyrhizus* appeals to some consumers more than that of *H. undatus.* Selected hybrids produced by inter- or intra-specific crossings are also cultivated, usually on a local basis and on a small scale (Mizrahi and Nerd 1999; Ortiz 1999; Canto 2000).

Selenicereus megalanthus

The fruit of *Selenicereus megalanthus* (yellow peel, white pulp), often known as "yellow pitaya" but also as pitahaya, is the most tasty vine cactus fruit (Mizrahi et al. 1997; Mizrahi and Nerd 1999). The first country to grow this species for export was Colombia at the request of a Japanese businessman, who appreciated the fruit. Significant planting started in Colombia in 1986 and export to Japan started in 1989 but soon ceased due to pests (eggs and larvae of insects) found where the corolla connects to the fruit. Fruit was then exported to Europe, which is not as concerned with tropical pests and has become the most important export market for yellow pitaya (also now shipped from Ecuador via Colombia). Planted areas in Colombia reached 4,000 ha in 1990 but later were reduced to 250 ha as result of disease problems, such as fusarium (which attacks the plant) and especially *Drechslera cactivora* (which infects the base of the pre-mature fruit and induces yellowing; Valera et al. 1995; Bibliowicz and Hernandez 1998). Accessions introduced into Israel from Colombia, although similar in morphology, vary in fruit characteristics and growth behavior, indicating different genotypes (growers in Colombia do not keep track of the origin of the material used for planting). This has been confirmed by DNA finger-printing analysis developed for vine cacti (Tel-Zur et al. 1999). Fruit of *S. megalanthus* obtains prime prices in Europe, higher than any other cactus fruit, due to its delicious taste (Ortiz 1999; Canto 2000; J. Rosenbaum, personal communication). Other yellow-peel vine cacti are available—some clones of *Hylocereus undatus* from Mexico and *H. costaricensis* from Nicaragua—whose qualities are similar to that of the common red-peel clones of these species. The present sources of fruit of *S. megalanthus* shipped to Europe are Colombia, Ecuador, and Israel.

Stenocereus *and* Cereus

Stenocereus spp. are cultivated only in Mexico. The fruits are tasty, resembling those of figs. Usually they are collected and sold in close proximity to where they are harvested and their price is relatively low (Benz et al. 1997). When they reach Mexico City, their price can be as high as U.S. $6 per kilogram. In the 1990s, efforts were directed to converting them into sustainable fruit crops (Pimienta-Barrios and Nobel 1994; Casas et al. 1997, 1999a,b; Pimienta-Barrios et al. 1997). The total cultivated area for *Stenocereus* spp. in Mexico exceeds 2,000 ha. The main limiting factors are the short storage and shelf life, in large measure because



Figure 11.5. Three-year-old orchard of *Cereus peruvianus* established near the southern coast of Israel.

of the tendency of the fruit to split during ripening. *Cereus peruvianus* is under domestication in Israel (Fig. 11.5) and is sold in Europe. The fruit lacks spines, has much longer storage and shelf life than that of *Stenocereus,* and is similar to that of *S. megalanthus.* As an index of the acceptability of such new cactus fruits, *C. peruvianus* was marketed for the first time in 1998 and was accepted very well in both local and European markets, due to its beautiful appearance, delicate sour-sweet taste, and unique aroma. Among eight clones released for cultivation in Israel, only two have proved to be promising for further planting. Unlike the others, their fruits do not tend to split upon ripening or to develop black spots under storage; similar efforts to develop the cultivation of *C. peruvianus* exist in California and Texas.

Conclusions and Future Prospects

Pitahayas and pitayas, unlike many other new crops, are appealing to consumers unfamiliar with the fruit because of their delicate texture and taste and their unusual and attractive appearance. Slow growth and development of the plants, low fruit yields, and especially the very short shelf life of the fruit (about 2 days) limit wide cultivation of *Stenocereus* species; commercial plantings occur in their area of distribution, and fruits are mainly marketed locally by growers and by people collecting fruits from wild plants. However, pitahayas and *Cereus peruvianus* are promising new worldwide crops. They have precocious and high yields and a longer fruit shelf life, which enables marketing of the fruit over long distances. Indeed, their cultivation is rapidly spreading around the world, and their fruits are available in supermarkets and specialty shops.

Pitahayas and pitayas increase the diversity of cultivated fruit crops, which may be used either for sustainable agriculture systems (e.g., *Stenocereus queretaroensis;* Fig. 11.2) or for the intensive fruit industry (e.g., *Hylocereus undatus;* Fig. 11.1). These cacti can compete successfully in profitability with common fruit crops. Because of the high water-use efficiency of Crassulacean acid metabolism (CAM) (Nobel 1994), the low water demand of pitahayas and pitayas represents a significant advantage in arid and semiarid regions not only because of the direct water savings but also because the environmental damage caused by heavily irrigated common crops is avoided. Pitahayas can also be used as sources for new products, such as colorants and polysaccharides for the food industry or their edible flowers.

The recent expansion of fruit crops from vine and columnar cacti has been based mostly on wild plants from southern North America (Mexico), central America, and northern South America (Colombia), where these fruits are traditionally used by local people. The plants are found mainly in home gardens or on marginal lands. Thus, professional breeding of improved cultivars should be an important objective, because most of the available material is a result of superficial selection based on a few visible traits.

Definition of the available plant material by taxonomic, molecular, and genetic studies is essential for these breeding efforts. Intergeneric and interspecific crosses are easily achieved among vine cacti, so growers can utilize hybrids as well as unidentified material as future cultivars. However, the appearance of diverse types of fruits in the markets can lead to confusion and marketing problems. The lack of distinct common names for existing crops (Table 11.1) already causes confusion for marketing.

Much research is required in order for pitahayas and pitayas to be established successfully as world crops. Horticultural treatments as well as orchard management practices have to be developed. Improved postharvest treatment is important. Pitahayas growing in structures are convenient candidates to be fed with CO_2; stomata open for CAM plants during the night when CO_2 enrichment can be done without overheating problems. The dramatic development of pitahayas and pitayas as fruit crops supports the recent trends to develop ethnic fruits as new crops and to utilize the underexploited cactus family as a source of new crops. Unlike some other new crops, a large gap exists between research and the commercialization of pitahayas and pitayas—a gap that must be filled for successful cultivation.

Literature Cited

Alvarez, M., S. C. Costa, H. Utumi, A. Huber, R. Ber, and J. D. Fontana. 1992. The anionic glycan from the cactus *Cereus peruvianus*—structural features and potential uses. *Applied Biochemistry and Biotechnology* 34: 283–295.

Alvarez, M., S. C. Costa, A. Huber, M. Baron, and J. D. Fontana. 1995. The cuticle of the cactus *Cereus peruvianus* as a source of a homo-alpha-D-galacturonan. *Applied Biochemistry and Biotechnology* 51: 367–377.

Barbeau, G. 1990. La pitahaya rouge, un nouveau fruit exotique. *Fruits* 45: 141–147.

Beard, C. E. 1937. Some chromosome complements on the Cactaceae and a study of meiosis in *Echinocereus papillosus. Botanical Gazette* 99: 1–21.

Benz, B. F., F. M. Santana, J. E. Cevallos, E. M. Munoz, J. A. Rosales, and M. A. Rosales. 1997. The structure and productivity of relict stands of pitaya (*Stenocereus queretaroensis;* Cactaceae), Jalisco, Mexico. *Economic Botany* 51: 134–143.

Bibliowicz, A., and S. M. Hernandez. 1998. *Organismos Fungosos Presentes en las Estructuras Reproductivas de la Pitaya Amarilla.* Universidad Nacional de Colombia, Santafé de Bogotá.

Britton, N. L., and J. N. Rose. 1963. *The Cactaceae: Description and Illustrations of Plants of the Cactus Family.* Vols. I & II. Dover Publications, New York.

Cacioppo, O. G. 1990. Pitaya: una de las mejores frutas producida por Colombia. *Informative Agroeconómico, Febrero:* 15–19.

Canto, A. R. 2000. *Pitahayas. Estado Mundial de su Cultivo y Comercialización.* Fundacion Yucatan Produce, Universidad Autónoma, Chapingo, Mexico.

Casas, A., B. Pickersgill, J. Caballero, and A. Valiente-Banuet. 1997. Ethnobotany and domestication in Xoconochtli, *Stenocereus stellatus* (Cactaceae), in the Tehuacan Valley and La Mixteca Baja, Mexico. *Economic Botany* 51: 279–292.

Casas, A., J. Caballero, A. Valiente-Banuet, J. A. Soriano, and P. Davila. 1999a. Morphological variation and the process of domestication of *Stenocereus stellatus* (Cactaceae) in central Mexico. *American Journal of Botany* 86: 522–533.

Casas, A., A. Valiente-Banuet, A. Rojas-Martinez, and P. Davila. 1999b. Reproductive biology and the process of domestication of the columnar cactus *Stenocereus stellatus* in central Mexico. *American Journal of Botany* 86: 534–542.

Deoliveira, S. A., M. D. P. D. Machado, A. J. Prioli, and C. A. Mangolin. 1995. In-vitro propagation of *Cereus peruvianus* Mill (Cactaceae). *In Vitro Cellular and Developmental Biology—Plant* 31: 47–50.

Feng-Ru, C., and Y. Chung-Ruey. 1997a. Flowering and fruit growth of pitaya (*Hylocereus undatus* Britt. & Rose). *Journal of the Chinese Society of Horticultural Science* 43: 314–321 (Chinese with English summary).

Feng-Ru, C., and Y. Chung-Ruey. 1997b. Forcing pitaya (*Hylocereus undatus* Britt. & Rose) by chemicals and controlled daylength and temperature. In *Proceedings of the Symposium on Enhancing Competiveness of the Fruit Industry.* Taipei, Taiwan. Pp. 163–190. (Chinese with English summary.)

Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer.* Harvard University Press, Cambridge, Massachusetts.

Haber, W. A. 1983. *Hylocereus costaricensis* (pitahaya sylvestre, wild pitahaya). In *Costa Rican Natural History* (D. H. Janjen, ed.). University of Chicago Press, Chicago. Pp. 252–253.

Infante, R. 1992. In vitro axillary bud proliferation and somatic embryogenesis of yellow pitaya *Mediocactus coccineus* (Salm-Dyck). *Plant Cell, Tissue, and Organ Culture* 31: 155–159.

IOS. 1986. The genera of the Cactaceae: Towards a new consensus. *Bradleya* 4: 65–78.

Lichtenzveig, J., S. Abbo, A. Nerd, N. Tel-Zur, and Y. Mizrahi. 2000. Cytology and mating systems in the climbing cacti *Hylocereus* and *Selenicereus. American Journal of Botany* 87: 1058–1065.

Machado, M. D. P. S., and A. J. Prioli. 1996. Micropropagation of *Cereus peruvianus* Mill (Cactaceae) by areole activation. *In Vitro Cellular and Developmental Biology—Plant* 32: 199–203.

Metz, C., A. Nerd, and Y. Mizrahi. 2000. Viability of pollen of two fruit cacti of the genus is affected by temperature and duration of storage. *HortScience* 35: 22–24.

Mizrahi, Y., A. Nerd, and P. S. Nobel. 1997. Cacti as crops. *Horticultural Reviews* 18: 291–320.

Mizrahi, Y., and A. Nerd. 1999. Climbing and columnar cacti: New arid land fruit crops. In *Perspectives on New Crops and New Uses* (J. Janick, ed.). American Society of Horticultural Science, Alexandria, Virginia. Pp. 358–366.

Moran, V. C. 1953. *Selenicereus megalanthus* (Schumann) Moran. *Gentes Herbarum* 8: 325.

Moran, V. C., and H. G. Zimmerman. 1991. Biological control of cactus weeds of minor importance in South Africa. *Agriculture, Ecosystems & Environment* 37: 37–55.

Nerd, A., and Y. Mizrahi. 1997. Reproductive biology of cactus fruit crops. *Horticultural Reviews* 18: 321–346.

Nerd, A., and Y. Mizrahi. 1998. Fruit development and ripening in yellow pitaya. *Journal of the American Society of Horticultural Science* 123: 560–562.

Nerd, A., and Y. Mizrahi. 1999. The effect of ripening stage on fruit quality after storage in yellow pitaya. *Postharvest Biology and Technology* 15: 99–105.

Nerd, A., E. Raveh, and Y. Mizrahi. 1993. Adaptation of five columnar cactus species to various conditions in the Negev Desert of Israel. *Economic Botany* 47: 304–311.

Nerd, A., F. Gutman, and Y. Mizrahi. 1999. Ripening and postharvest behavior of fruits of two *Hylocereus* species (Cactaceae). *Postharvest Biology and Technology* 17: 39–45.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nobel, P. S. 1994. *Remarkable Agaves and Cacti.* Oxford University Press, New York.

Nobel, P. S., and E. Pimienta-Barrios. 1995. Monthly stem elongation for *Stenocereus queretaroensis*—relationships to environmental conditions, net CO_2 uptake, and seasonal variations in sugar content. *Environmental and Experimental Botany* 35: 17–24.

Ortiz, Y. H. 1999. *Pitahaya, a New Crop for Mexico.* Editorial Limusa, Mexico City.

Pimienta-Barrios, E. 1999. *El Pitayo en Jalisco* y *Especies Afines en México.* Universidad de Guadalajara, Zapopan, Mexico.

Pimienta-Barrios, E., and P. S. Nobel. 1994. Pitaya (*Stenocereus* spp. Cactaceae)—An ancient and modern fruit crop of Mexico. *Economic Botany* 48: 76–83.

Pimienta-Barrios, E., and P. S. Nobel. 1995. Reproductive characteristics of Pitayo (*Stenocereus queretaroensis*) and their relationship with soluble sugars and irrigation. *Journal of the American Society of Horticultural Science* 120: 1082–1086.

Pimienta-Barrios, E., P. S. Nobel, C. Robles-Murguia, L. Mendez-Moran, E. Pimienta-Barrios, and E. Yepez-Gonzalez. 1997. Ethnobotany, productivity, and ecophysiology of pitaya (*Stenocereus queretaroensis*). *Journal of the Professional Association for Cactus Development* 2: 29–47.

Raveh, E., M. Gersani, and P. S. Nobel. 1995. CO_2 uptake and fluorescence responses for a shade tolerant cactus *Hylocereus undatus* under current and doubled CO_2 concentrations. *Physiologia Plantarum* 93: 505–511.

Raveh, E., A. Nerd, and Y. Mizrahi. 1997. Responses of climbing cacti to different levels of shade and to carbon dioxide enrichment. *Acta Horticulturae* 434: 271–278.

Raveh, E., A. Nerd, and Y. Mizrahi. 1998. Responses of two hemiepiphytic fruit crop cacti to different degrees of shade. *Scientia Horticulturae* 53: 115–122.

Silva, W. R., and M. Sazima. 1995. Hawkmoth pollination in *Cereus peruvianus,* a columnar cactus from Southeastern Brazil. *Flora* 190: 339–343.

Silvius, K. M. 1995. Avian consumers of cardon fruits (*Stenocereus griseus,* Cactaceae) on Margarita Island, Venezuela. *Biotropica* 27: 96–105.

Spencer, J. L. 1955. A cytology study of the Cactaceae of Puerto Rico. *Botanical Gazette* 117: 33–37.

Taylor, N. P., and D.C. Zappi. 1992. Proposal to conserve *Cereus jamacaru* (Cactaceae) with a new type. *Taxon* 41: 590–591.

Tel-Zur, N., S. Abbo, D. Myslabodski, and Y. Mizrahi. 1999. Modified CTAB procedure for DNA isolation

from epiphytic cacti of the genera *Hylocereus* and *Selenicereus* (Cactaceae). *Plant Molecular Biology Reporter* 17: 249–254.

Varela, C. H., De. P. M. Sanchez, and N. Bravo. 1995. Etiological study of the "dry leaf rot" disease in yellow pitaya (*Selenicereus megalanthus*). *Fitopatologia Colombiana* 19: 40–47.

Wang, X. 1997. Biology of ripening of apple cactus (*Cereus peruvianus* [L.] Miller). Ph.D Thesis, Ben Gurion University of the Negev, Beer-Sheva, Israel.

Weiss J., A. Nerd, and Y. Mizrahi. 1994a. Flowering behavior and pollination requirements in climbing cacti with fruit crop potential. *HortScience* 29: 1487–1492.

Weiss J., A. Nerd, and Y. Mizrahi. 1994b. Flowering and pollination requirements in *Cereus peruvianus* cultivated in Israel. *Israel Journal of Plant Sciences* 42: 149–158.

Weiss, J., L. Scheinvar, and Y. Mizrahi. 1995. *Selenicereus megalanthus* (the yellow pitaya), a climbing cactus from Colombia and Peru. *Cactus and Succulent Journal (U.S.)* 67: 280–283.

Wu, M. C., and C. S. Chen. 1997. Variation of sugar content in various parts of pitaya fruit. *Proceedings of the Florida State Horticultural Science* 110: 225–227.

CHAPTER

› 12 ‹

FORAGE, FODDER, AND ANIMAL NUTRITION

Ali Nefzaoui and Hichem Ben Salem

Introduction
Increasing Usage of Cacti in Arid Zones
Use of Cacti as Fodder
Nutrient Contents
Intake and Digestibility
Cladode Consumption and Sheep Rumen Fermentation
Cladodes as a Water Source
Some Practical Considerations
Integration of Platyopuntias with Other Feed Resources in the WANA Region
Conclusions
Literature Cited

Introduction

The future of arid and semiarid regions depends on the development of sustainable agricultural systems and on the cultivation of appropriate crops. Such crops must successfully withstand water shortage, high temperature, and poor soil fertility. Cacti, particularly platyopuntias, can satisfy these requirements and are becoming increasingly important for both subsistence and market-oriented activities in arid and semiarid regions (Barbera 1995), as for vertebrates in natural ecosystems (Chapter 7). This chapter focuses on the West Asia/North Africa (WANA) region, large portions of which have winters with low and erratic rainfall and hot, dry summers. It is characterized by high population growth, limited areas of arable land, harsh deserts, and limited water resources for irrigation development (Nordblom and Shomo 1995). The WANA region contains most of the more than 1 million hectares (ha) utilized worldwide (Table 12.1) for raising platyopuntias—principally *Opuntia ficus-indica*—for forage (consumption *in situ*) and fodder (consumption after harvest and transport) for livestock

As much as 50% of arid rangeland in the WANA region may have lost its vegetation since World War II, while concomitantly the human population has increased fourfold (Le Houérou 1991). In this regard, the sheep population has increased by 75% and the stocking rate has jumped from one sheep per 4 ha to one sheep per ha between 1950 and 1989. Indeed, the contribution of such rangelands to the annual feed requirements of livestock is in decline, going from 80% in 1965 to less than 25% of the requirement in 2000. Overgrazing and range deterioration have forced pastoralists to change their migration and feeding patterns. In some countries, the forage diet of animals is heavily supplemented with barley grain and other commercial concentrated feeds. A typical feed calendar for

TABLE 12.1
Estimated land areas utilized for raising cacti, mainly *Opuntia ficus-indica*, for forage and fodder

Region or country	Land area utilized (ha)
Brazil	370,000
Other South American countries	75,000
Mexico	230,000
Other North American countries	16,000
Southern Africa	2,000
WANA region	
Tunisia	500,000
Algeria	150,000
Other WANA countries (Morocco, Libya, Egypt, Jordan, Syria, Lebanon)	300,000

Data are from Le Houérou (1992), Nobel (1994), and various Ministry of Agriculture reports.

agropastoral systems of arid and semiarid regions of the WANA region also includes supplementation with cactus in May through September (Table 12.2).

The search for plant species with the ability to grow and produce in arid areas has been a permanent concern in most WANA countries. The characteristics of cacti fit most of the requirements of a drought-resistant fodder crop, as described by De Kock (1980): (1) the crop must not only be able to withstand long droughts, but it must also be able to produce large quantities of fodder during periods of favorable rainfall that can be utilized during drought periods; (2) the crop must have a high carrying capacity; (3) the crop must not have an adverse effect on the health of the animals consuming it; (4) extensive utilization should not have an adverse effect on the plants, i.e., the plants must have high recovery ability; (5) establishment and maintenance of the plantations must be cost effective and should have a low initial cost; and (6) the crop must be relatively undemanding with respect to soil and climatic requirements. Using these criteria, *Opuntia ficus-indica* has proved to be an important fodder crop in Tunisia, such as for feeding sheep (Fig. 12.1).

Increasing Usage of Cacti in Arid Zones

Cacti grow in "deserts" and are drought tolerant. Indeed, they possess a specialized photosynthetic mechanism, which leads to a more efficient production of dry matter per unit water consumed than that of grasses or legumes (Russell and Felker 1987; Nobel 1988, 1989; Chapter 4). Cacti produce fodder, fruit, and other useful products. They also can prevent the long-term degradation of ecologically weak environments. Cacti in general and *Opuntia* spp. in particular were introduced into the WANA region by Spanish moors in the 16th century (Le Houérou 1992). Nevertheless, only toward the end of the 20th century have large plantations been established. These create evergreen fodder banks to feed animals during drought and combat desertification as well.

Opuntia spp. used for animal feeding are abundant, easy and cheap to grow, palatable, and able to withstand prolonged droughts (Shoop et al. 1977). Such characteristics make them a potentially important feed supplement for livestock, particularly during periods of drought and seasons of low feed availability. The cladodes constitute the majority of the biomass of a platyopuntia and can be fed to livestock as fresh forage or stored as silage for later feeding (Castra et al. 1977). In any case, the idea of using cactus to feed livestock is not recent. Griffith (1905) confirmed

TABLE 12.2
Common feed calendar for small ruminants in the WANA region

Months	Physiological stage	Area	Main type of feed	Supplement
May–July	Mating, early pregnancy	Agricultural land	Cereal stubble	Bran, barley, cactus
August–September	Pregnancy	Agricultural land	Cereal stubble, straw	Bran, barley, cactus, shrubs (*Atriplex*)
October–January	Late pregnancy, early lactation	Rangeland, agricultural land	Fallow, hay, natural grazing	Barley, wheat, bran, olive tree leaves and twigs
February–April	Weaning, fattening	Rangeland, agricultural land	Natural grazing, fallow, standing barley, straw	Olive tree leaves and twigs, barley, bran



Figure 12.1. Use of *Opuntia ficus-indica* for fodder in Tunisia: (A) Transport of cladodes from the field; (B) chopping of cladodes, which can be laborious; and (C) feeding chopped cladodes to sheep.

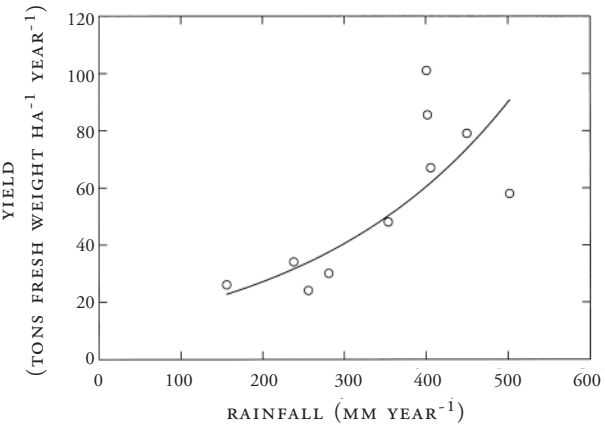


Figure 12.2. Productivity of spineless cactus (*Opuntia ficus-indica* var. *inermis*) versus rainfall in Tunisia. Adapated from Monjauze and Le Houérou (1965).

that feeding platyopuntias to livestock started in the United States before the Civil War (1861–1865). Cladodes were extensively transported from regions of Texas, such as Brownsville, Indianola, San Antonio, and Eagle Pass. Both natural and cultivated populations of platyopuntias have become important for fodder in many parts of the world. They are cultivated in Africa, Argentina, Bolivia, Brazil, Chile, Colombia, Israel, Italy, Mexico, Peru, Spain, and the United States (Curtis 1979; Le Houérou 1979; Brutsh 1984; Russell and Felker 1987; Clovis de Andrade 1990; Barbera et al. 1992; Flores Valdez and Aguirre Rivera 1992).

Large areas of platyopuntias are available year-round in Algeria, Mexico, and especially Brazil and Tunisia and serve as an emergency feedstock in case of drought (Table 12.1). In many arid areas (e.g., Tunisia, Mexico, South Texas, South Africa), farmers make extensive use of cacti as emergency forage, harvesting it from both wild and cultivated populations to prevent the disastrous consequences of frequent and severe droughts (Le Houérou 1992). Since 1900 in North Africa, shrubs (mainly *Acacia cyanophylla* and *Atriplex nummularia* or *A. halimus*) and cacti (mainly *Opuntia ficus-indica* var. *inermis*) have been planted to reduce water and wind erosion and rangeland degradation. Nearly 1 million ha have been planted in Algeria, Morocco, Libya, and Tunisia (Table 12.1). These plantations in low rainfall areas also provide feed for livestock during frequent drought periods. Because of their high water-use efficiency (Nobel 1988, 1989), the aboveground productivity of cacti tends to be much higher than that of most other plant species in arid and semiarid regions. For example, under rain-fed conditions in Tunisia and with no fertilizer application, spineless platyopuntia yields vary from 20 to 100 tons fresh weight of cladodes ha^{-1} year^{-1} as rainfalls increase from 150 to 400 mm per year (Fig. 12.2).

Marginal lands often represent fragile ecosystems. Ploughing and indiscriminate vegetation removal can result in large-scale degradation and destruction of vegetation cover. The scarcity and even disappearance of several plant species indicate the magnitude of genetic and edaphic losses (Le Houérou 1991). To reverse the desertification trend and to restore vegetation cover in such areas, appropriate integrated programs are needed for rangeland monitoring, livestock control, and conservation of natural resources.



Figure 12.3. Use of *Opuntia ficus-indica* to consolidate water harvesting along terraces in Tunisia.

Spineless cactus (*O. ficus-indica*), which is drought and erosion tolerant, is being advantageously and widely established in Tunisia and Algeria to slow and direct sand movement, to enhance the restoration of the vegetation cover, and to avoid the destruction by water of the land terraces built to reduce runoff (Fig. 12.3). In central and southern Tunisia, cactus plantations play a key role in natural resources conservation as well as provide a large amount of fodder for livestock. The strong rooting system of cacti helps stabilize land terraces. One or two rows of cladodes are planted on the inner side of the terraces (Fig. 12.3). The rooting system is enhanced by the collection of the water at the base of the terrace. Roots are widespread on the elevated part of the terrace and go deeply into the soil, ensuring stability of the terraces. As an additional benefit, cut and carried cladodes from such plantings provide sufficient feed resources during dry spells. Platyopuntias are also used in combination with cement barriers or cut palm fronds to stop wind erosion and sand movement.

Use of Cacti as Fodder

Nutrient Contents

Platyopuntias are an unbalanced feed nutrientwise but a cost-effective source of energy and water. Cladodes are low in crude protein, fiber, phosphorus, and sodium (Le Houérou 1992; Nefzaoui et al. 1995). Therefore, diets containing cactus should be balanced for these nutrients by appropriate supplements. The water content on a fresh-weight basis averages nearly 90% (Table 12.3). The ash content is about 20% of the dry weight. The crude protein is often below 5% but can be up to 10% of the dry weight (Table 12.3). The fiber content is also relatively low, about 10% of the dry weight. The nitrogen-free extract, which includes monomeric and polymeric sugars, is about 60% of the dry weight (Table 12.3). Cladodes' low content of phosphorous (P; about 0.03% of the dry weight) and sodium (Na; about 0.01%) requires supplementation when they are fed to animals.

The ash content of cladodes is high (Table 12.3), mainly because of the high calcium (Ca) content. High Ca levels in soils in arid and semiarid regions cause cacti to accumulate high quantities of Ca compounds (Nobel 1988). Platyopuntia cladodes also have high levels of oxalates (Ben Salem et al. 2002). For example, the oxalate amount is about 13% of the dry weight and 40% is in soluble form (the high amount of oxalates may explain the laxative effect of cladodes when fed to animals). The oxalates mostly contain Ca, making this cation less available to animals. Nevertheless, the Ca content of cladodes is generally higher than animal requirements. An excess of Ca is not a problem *per se,* but an unbalanced Ca:P ratio, which is generally about 35 for cladodes, needs to be corrected. Indeed, Shoop et al. (1977), working with *Opuntia polyacantha,* indicated that its P content is below livestock dietary requirements. In particular, Ca levels are adequate but the Ca:P ratio of about 36 is too high for optimal livestock performance. De Kock and Aucamp (1970) reported the same problem with *O. ficus-indica* and suggested using licks for P and Na. These licks may be made from the following ingredients: salt, monosodium phosphate, molasses, dicalcium phosphate, and bonemeal. According to Shoop et al. (1977), most other minerals in cladodes (e.g., manganese, copper, zinc, magnesium, and iron) have concentrations within the range generally acceptable in the diets of ruminants. An exception is sodium content, which is relatively low (0.02% for *O. polyacantha*).

Crude fiber content (Table 12.3) is actually a poor indicator of feed fiber quality. For instance, the fibers cellulose and lignin have low digestibility. For five platyopuntias (*Opuntia engelmannii, O. filipendula, O. fragilis, O. polyacantha,* and *O. versicolor*), cellulose averages 11 ± 2% (mean ± 1 standard deviation) of the dry weight, hemicellulose averages 18 ± 3%, and lignin averages 3.9 ± 0.7% (Ben Thlija 1987); in comparison, for alfalfa these values are 22%, 15%, and 7.9%, respectively.

Although the protein content of cladodes is generally low (Table 12.3), it tends to increase after nitrogen fertilization. For instance, N and P fertilizers can increase crude protein contents of *Opuntia* cladodes from 4.5 to 10.5% of the dry weight (Gonzalez 1989). Also, Gregory and Felker (1992) found that some clones from Brazil have over 11% crude protein. In the WANA region, large plantations of *Opuntia* are utilized for fodder production in dry areas where soil quality, rainfall, and finances argue

TABLE 12.3
Mean chemical composition of platyopuntia cladodes used for forage or fodder

Species	Water (% of fresh weight)	Ash	Crude protein	Crude fiber	N-free extract	Ca	Mg	P	K	Na
		(% of dry weight)								
Opuntia engelmannii, O. lindhymeri[a]	85		2.9			8.3	1.6	0.04	3.0	
O. ficus-indica										
various[b]	89	17	4.8	10.9	65					
California[c]	90		10.4		64	6.3	1.4	0.033	1.2	0.0031
Chile[c]	89		8.9			3.9	1.3	0.012	2.0	0.0030
Tunisia[d]	87	27	3.8	8.6	58	8.7		0.04	1.1	0.05

[a] Hoffman and Walker (1912)
[b] Lozano (1958); De Kock (1965); Theriez (1965); Teles (1978)
[c] Nobel (1988)
[d] A. Nefzaoui (unpublished observations)

against fertilizer application. Therefore, increasing the nitrogen content of cladodes through selection or hybridization is more promising. Protein deficiency can also be solved through appropriate supplementation and/or feed combinations. Wehren (1976) showed that the amino acid composition of cladodes of *O. ficus-indica* var. *inermis* is quite satisfactory for animals; the proteins of three cultivars contained an average of 10.6% aspartic acid, 13.0% glutamic acid, 4.3% threonine, 4.3% serine, 6.5% proline, 4.8% glycine, 7.8% alanine, 0.8% cystine, 7.0% valine, 2.1% methionine, 5.2% isoleucine, 8.3% leucine, 4.1% tyrosine, 5.1% phenylalanine, 5.9% lysine, 2.3% histidine, and 5.5% arginine.

The nutritive quality of *Opuntia* cladodes depends on plant type (species, varieties), cladode age, season, and agronomic conditions (e.g., soil type, climate, and growing conditions). In Tunisia, the percentage dry weight is highest and crude protein content is lowest during the summer season; the ash content tends to be highest in the spring and crude fiber content highest in the winter (Ben Salem et al. 1996b). The percentage dry weight increases as cladodes age. Also, when cladode age increases from 1 to 5 years, crude protein content of *O. ficus-indica* var. *inermins* decreases (from 5 to 3% of dry weight) and crude fiber increases (from 9 to 20%; A. Nefzaoui, unpublished observations). This trend is similar to that for other fodder sources, where nutrients decrease with plant age resulting from the relative increase in fiber content (Nefzaoui and Ben Salem 1998).

Intake and Digestibility

Animals can consume large amounts of cladodes. For instance, Jersey cows fed on cladodes and supplemented with 1 kg day^{-1} of concentrated feed consume 51 kg fresh weight day^{-1} of the cladodes (Woodward et al. 1915). Metral (1965) similarly found a voluntary intake of 60 kg day^{-1} when cladodes alone are fed to cows. Viana (1965) reported an average voluntary intake of 77 kg day^{-1} for cows. For sheep, Monjauze and Le Houérou (1965) reported cladode intakes of 2.5 to 9 kg day^{-1}. Valdez and Flores (1967) observed higher intake with *O. ficus-indica* (11 kg day^{-1}) than with *O. robusta* (6.5 kg day^{-1}). Intakes are higher when the water content of the cladodes is high (A. Nefzaoui and H. Ben Salem, unpublished observations). Cladode consumption can have a laxative effect on sheep, leading to a more rapid passage of the food through the animal's digestive tract. This leads to poorer digestion, especially when the cladodes constitute more than 60% of the dry matter intake; supplementing with fibrous feed (e.g., straw or hay) can alleviate such laxative effects.

Sheep fed straw consume up to 600 g dry weight of cladodes without any digestive disturbance (Cordier 1947). Supplementation of poor quality roughages with molasses increased their palatability (Preston and Leng 1987; Rangnekar 1988), so cladodes with their high carbohydrate contents may have similar effects as molasses. The energy content of cladodes is 3,500 to 4,000 kcal kg^{-1} dry weight, just over half of which is digestible and comes mainly from

TABLE 12.4

Effect of supply of spineless *Opuntia ficus-indica* var. *inermis* on intake and digestibilities by sheep fed straw-based diets in Tunisia

	Amount of cladodes (g dry weight day^{-1})				
	0	*150*	*300*	*450*	*600*
Dry weight intake (g day^{-1})					
Straw	550a	574ab	523a	643bc	716c
Cactus + straw	550a	724b	823c	1,093d	1,278e
Total digestibility					
Organic matter	45a	50ab	54b	58b	59b
Crude protein	50a	55ab	54ab	59bc	64c
Crude fiber	53a	51a	53a	52a	47a
Digestible intakes (% of maintenance requirements)					
Organic matter	93	123	158	193	212
Crude protein	52	52	64	93	111
Protozoa (10^4 per ml)	3.5a	9.3b	13.0c	17.7d	13.1c
Degradability of cellulose (%)	85	72	57	55	56

Means in the same row followed by different letters differ ($P < 0.05$). Data are from Ben Salem et al. (1996).

carbohydrates (De Kock 1983; Ben Thlija 1987). In arid and semiarid regions of North Africa, cereal crop residues and natural pastures generally do not meet the nutrient requirements of small ruminants for meat production. Cladodes can provide a cost-effective supplementation, such as for raising sheep and goats on rangelands. For instance, when diets of grazing sheep are supplemented with cladode cakes, the daily weight gain increases nearly 50% (to 145 g day^{-1}; Tien et al. 1993); when cladodes are supplied to grazing goats that have access to alfalfa hay, the milk yield is increased by 45% (to 436 g day^{-1}; Azocar et al. 1991). When cladodes are associated with a protein-rich feedstuff, they may replace barley grains (Ben Salem et al. 1998) or maize silage (Metral 1965) without affecting sheep and cattle daily weight gains. For instance, milk yield for lactating goats supplied with 2.2 kg alfalfa hay day^{-1} is actually slightly higher (1,080 g day^{-1}) when 0.7 kg cladodes replaces an equal mass of alfalfa (Azocar et al. 1996).

When sheep are offered increasing amounts of cladodes, their intake of the accompanying straw also increases (Table 12.4). The dry matter intake of straw plus cladodes steadily increases as the amount of cladodes supplied increases. The cladodes are highly digestible, with similar digestibilities for organic matter, crude protein, and crude fiber, ranging from 45 to 64% (Table 12.4). Digestibility of cladodes by sheep is similar to that for common forage crops. The main difference between platyopuntias and other forage crops is the timing of the degradability of nutrients in the rumen. For other forage crops, maximal degradability in the rumen requires about 48 hours, whereas nutrients in cladodes are degraded very rapidly (between 6 and 12 hours) and little additional nutrient extraction occurs after 24 hours (Ben Thlija 1987). Similarly, 80% of the total digestion of singed Great Plains prickly pear (*Opuntia polyacantha*) by cattle occurs during the first 16 hours (Shoop et al. 1977).

A rapid rate of digestion leads to a faster passage of the material through the digestive tract, leading to more available volume for further intake. Because of the low gut fill of cladodes, an increase of cactus in the diet does not necessarily reduce the intake of other components of the ration (Table 12.4). This is of great importance for arid zones where livestock is fed mainly with straw or cereal stubble, which are low quality coarse feeds that have poor intakes, resulting in low animal daily weight gains. In feeding trials with heifers in the United States, cladodes are more readily and more completely digested than is grass-hay (*Agropyron cristatum* and *Bromus* spp.). In South Africa, the yields (tons fresh weight ha^{-1} year^{-1}) and digestible nutrients (tons fresh weight ha^{-1} year^{-1}) can be 80 and 5.0 for *O. ficus-indica,* 25 and 4.2 for *Zea mays* (maize silage), and 5 and 2.5 for dried lucerne hay (Rossouw 1961), suggesting a superiority of the platyopuntia as a forage.

Cladode Consumption and Sheep Rumen Fermentation

Ben Salem et al. (1996a) studied the effect of increasing the level of spineless cladodes on rumen fermentation in sheep given straw *ad libitum.* The cactus improves rumen fermentation (Table 12.4), as also occurs for sheep on an *Acacia cyanophylla*–based diet supplemented with cladodes and urea (Ben Salem 1998). In both cases the rumen fluid pH is not affected by up to 600 g dry weight of cladodes day^{-1}, remaining at 6.9 ± 0.1. The cladodes are rich in easily fermentable carbohydrates, and their consumption probably enhances salivation.

Compared with a cactus-free diet, the highest supply of cladodes doubles the concentration of ammonia nitrogen in the rumen of sheep fed diets based on straw (Ben Salem et al. 1996a) or acacia (Ben Salem 1998). This leads to ammonia concentrations near optimal for microbial growth and fiber digestion in the rumen (Satter and Slyter 1974; Ushida and Jouany 1985). Indeed, the protozoa counts per volume increases fourfold as the amount of cladodes ingested exceeds 300 g dry weight day^{-1} (Table 12.4). Adding cladodes to the diet can increase the volatile fatty acids (such as propionic acid) by up to 30%, reflecting the increased intake of soluble carbohydrates.

Ben Salem et al. (1996a) used an *in sacco* technique (Ørskov et al. 1980) to study the effect of cladode supply on cellulolytic activity in the rumen of sheep on a straw-based diet. Nylon bags (pore size of 46 µm) are filled with specified amounts of cladodes and straw, incubated in the rumen for various times, and then removed and the dry weights of the various fractions determined. The degradability of cellulose is adversely affected by increasing amounts of cladodes in the diet (Table 12.4), although the rate of degradation is not affected (Ben Salem et al. 1996a). The impairment of cellulolytic activity in the rumen as the cladode intake increases may be because the increasing ciliate protozoa have a negative effect on the number of bacteria in the rumen and thus on cellulose degradation (Demeyer and Van Nevel 1979). The high level of minerals in cladodes may also decrease microbial growth in the rumen (Komisarczuk-Bony and Durand 1991). In any case, a combination of *O. ficus-indica* and cereal straw is a nutritionally satisfactory solution for maintaining small ruminants in arid regions. Indeed, supplying cladodes can improve the nutritive value and intake of the poor quality roughages.

Cladodes as a Water Source

Water scarcity can depress feed intake, digestion, and therefore weight gains of sheep and goats (Wilson 1970; El-Nouty et al. 1988; Silanikove 1992). Thus, supplying livestock with water during the summer and during drought periods is crucial in the WANA region and other arid regions. Animals consume considerable energy to reach water points. Moreover, rangeland degradation in the area surrounding water points is a serious problem. Therefore, the high water content of cladodes is beneficial in dry areas. Cattle given abundant supplies of cladodes require little (Cottier 1934) or no (Woodward et al. 1915) additional water. Sheep fed for a long period (400 to 500 days) with large amounts of cladodes stop drinking (Roussow 1961; Harvard-Duclos 1969). Also, water intake by sheep on a wheat straw diet becomes extremely low when the daily intake of cladodes is 300 g dry weight day^{-1} or more (Fig. 12.4), consistent with other findings (Terblanche et al. 1971). Similarly, sheep on an *Acacia cyanophylla* diet require 1.2 liter water day^{-1} when supplemented with barley but only 0.6 liter day^{-1} when supplemented with cladodes (Ben Salem et al. 2002).

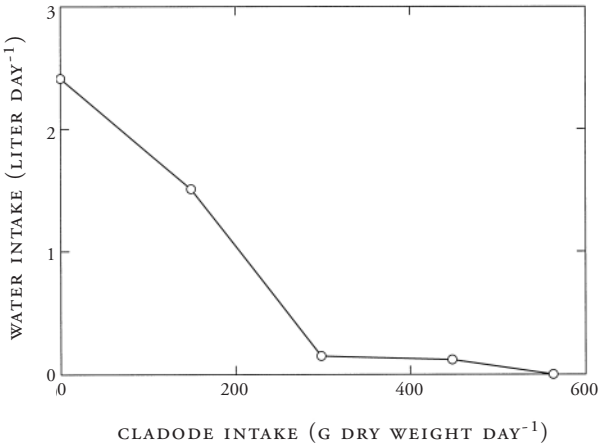


Figure 12.4. Influence of cladode consumption on daily water uptake by sheep. Data are from Ben Salem et al. (1996).

Some Practical Considerations

The method of utilization of cladodes for livestock will differ according to circumstances, such as available labor, facilities, and quantity of cactus available. Although grazing of cladodes *in situ* is the simplest method, it is not the most efficient and care should be taken so that the animals do not overgraze the plants. The harvested cladodes may be cut into small pieces or strips and fed in a confined area to limit wastage (Fig. 12.1C). The cladodes can also be cut into smaller pieces and mixed with hay or low-quality alfalfa to make silage (if no fruits are included, molasses is usually added), which is maintained anaerobically.

Cladodes fed in various forms can keep animals alive for long periods. To supplement cladodes fed *ad libitum,* alfalfa or hay can provide protein and a lick of equal parts by mass of bone meal, salt, and fodder lime can provide phosphate and sodium (De Kock 1983).

It is cheapest to store cladodes as parts of living plants instead of after harvesting. Once harvested, chopped cladodes can be dried and then ground, e.g., using a hammermill with a sieve having 6-mm-diameter pores. Cladodes in the form of meal are not only more easily ingested but also are easier to store for use during droughts. Good quality silage can be made by chopping the pads together with oat straw, low-grade lucerne hay, or other roughage using 84 parts by mass of cladodes and 16 of roughage with the addition of 2% molasses.

The easiest and cheapest way to utilize platyopuntias is grazing. However, overgrazing of the plantation must be guarded against. Young plants are especially susceptible to overgrazing and can be killed by sheep. Even older plants can be so badly damaged that the subsequent production will be considerably lower. The best method for grazing is to divide the plantation into small paddocks and to graze each of these intensively for a few months every 3 years or so. Direct browsing necessitates a very tight control on grazing, otherwise wastage may reach 50% of the fodder produced (cladodes partially eaten and abandoned) and the plantation itself may be destroyed by overbrowsing (Monjauze and Le Houérou 1965; De Kock 1980). This type of management has a very low cost and the grass between the shrubs is available to the stock. Plants in a paddock can be grazed to one cladode higher than the original planting so that the plants recover well, the material used is of good quality, and the plants are kept within a usable size. Zero grazing—the cut-and-carry technique—has the opposite consequences. Loss of feed is virtually nil and risk of overutilization is small, except when young plantations are harvested too early. Even though the zero-grazing technique is labor-intensive, in most cases in North Africa it is the recommended method because of insufficient grazing discipline.

Although spineless *O. ficus-indica* is easiest to use, cladodes with spines are also valuable feed provided the spines are singed off first, usually through the use of a propane burner (Shoop et al. 1977). In Texas and Mexico, the standing plant is singed, whereas in North Africa detached cladodes are singed and then chopped into small pieces by hand (Fig. 12.1B) or machines. Steaming to moisten the spines and chopping of large pads can also facilitate the consumption of cladodes by livestock (Griffiths 1905).

Integration of Platyopuntias with Other Feed Resources in the WANA Region

In the WANA region climatic conditions lead to two feed gaps each year (Table 12.1): (1) in the winter (2–4 months) and (2) an even larger one in the summer plus autumn (5–6 months). These gaps require large amounts of supplemental feed. National strategies aimed to increase rangeland productivity have focused on highly producing species, such as *Acacia cyanophylla, Atriplex nummularia* (or *A. halimus*), and spineless platyopuntias. Several techniques for planting shrubs and cacti are used: (1) on communal rangelands, where introduced species are planted in rows without removal of natural herbaceous or woody natural species; (2) on private land an alley-cropping technique is preferred, where farmers can cultivate the area between rows when the rainfall conditions are favorable; (3) when soil conservation is crucial (Fig. 12.3), plantings are done for both types following the contour lines; and (4) the oldest type ("bosquet") involves a dense planting of platyopuntias around the house for fruit and for fodder for animals. Clearly, integrating platyopuntias with other resources in the feeding system is beneficial.

Poor-quality roughage may be supplemented with cladodes of *Opuntia ficus-indica* var. *inermis.* Indeed, the intake of straw goes up significantly with the increase of the amount of cladodes in the diet (Nefzaoui et al. 1993; Ben Salem et al. 1996). Cladodes are also a good supplement to ammonia- or urea-treated straw, because they provide the necessary soluble carbohydrates for the efficient use of nonprotein nitrogen in the rumen (Nefzaoui et al. 1993). For Barbarine sheep, voluntary intake of cladodes (presented *ad libitum*) remains high (450 g dry weight day^{-1}) when 250 or 480 g day^{-1} of untreated, urea- or ammonia-treated straw is ingested (Nefzaoui et al. 1993). Diets containing 64% cladodes and straw cause no digestive disturbance. Maintenance energy requirements for sheep are met with the low level of straw intake, and for high level the energy intake is 80% above the maintenance level. Urea- or ammonia-treated straw is necessary to reduce the nitrogen deficit. When the untreated straw plus cladode diet is supplemented with *Atriplex nummularia* (about 300 g dry weight day^{-1}) as the nitrogen source, even more nitrogen is retained in the sheep and the digestibility of organic matter and crude protein exceeds 70% (Nefzaoui and Ben Salem 1996). For 4-month-old lambs, when cladodes replace the more expensive barley grain, 10 to 15% more organic matter is taken up and daily weight gain averages 15% higher (Table 12.5). Platyopuntias such as *O. ficus-indica* can also be important for goats raised under

TABLE 12.5

Intake, digestibility, nitrogen balance, and growth for lambs on straw-based diets supplemented with conventional feeds (barley and soybean meal) and alternative feeds (*Opuntia ficus-indica* and *Atriplex nummularia*)

	Supplements			
	Soybean meal		Atriplex	
Quantity	Barley	*Opuntia*	Barley	*Opuntia*
Organic matter intake (g per [kg body weight]$^{0.75}$)	68	85	81	94
Digestibility (%)				
Organic matter	70	71	68	75
Protein	73	71	71	73
Fiber	68	69	68	74
Retained N (g day^{-1})	9.4	9.5	7.5	12.2
Daily weight gain (g day^{-1})	108	119	59	81

Data are for Tunisia and are from Ben Salem et al. (1998).

harsh conditions. Supplementing Alpine × local goats on native rangeland with cladodes and *A. nummularia* (100 g dry weight of each per day) substantially increases the daily weight gains of these animals (by 25–60 g day^{-1}; Ben Salem et al. 2000), so fresh *O. ficus-indica* and other nonconventional feeds can have economic advantages for livestock feeding.

Conclusions

Cladodes can be an important fodder in the WANA region, as clearly shown for sheep. Cladodes are not a balanced feed, but are a good, inexpensive energy and water source. They are high in ash, Ca, soluble carbohydrates, and vitamin A, but low in crude protein, fiber, P, and Na; as cladodes age, they increase in dry matter and fiber but decrease in crude protein. As for other good forage crops, cladodes are highly digestible, with typical digestibilities of 60 to 70% for organic matter, 40 to 70% for crude protein, and 40 to 50% for crude fiber. When the level of cladodes in the diet increases, the intake of fibrous feeds, the rumen protozoa, and the rumen ammonia concentration increase while water intake and rumen cellulolytic activity decrease. Indeed, feeding cladodes can cause sheep essentially to stop drinking water. Cladodes are highly palatable—about 6 to 9 kg and 50 to 80 kg of dry weight can be consumed daily by sheep and cattle, respectively. Cladodes have a low gut fill value, because their intake does not reduce fibrous feed intake. The nutritive value of spiny and spineless cladodes are similar, and spines are readily removed. Cladodes should be supplemented with an appropriate and cost-effective nitrogen source (e.g., *Atriplex* spp.). Recommendations are (1) avoid decreasing rumen cellulolytic activity by adding molasses, (2) limit the amount of grain in the diet for the same reason, (3) feed animals fibrous feeds (straw, hay) before cactus to minimize any laxative effect, and (4) use a special mineral supplement for adequate amounts of sulfur. In any case, the high moisture content of cladodes alleviates the problem of watering animals in dry regions.

Acknowledgment

An earlier version of this material focusing less on international aspects and more on specific sheep diets and with different figures and tables appeared in the June 2000 CactusNet newsletter.

Literature Cited

Azocar, P. C., and H. C. Rojo. 1991. Uso de cladodios de tuna (*Opuntia ficus-indica*) como suplemento forragero estival de cabras en lactancia, en reemplazo de heno de alfalfa. *Avances en Producción Animal* 16: 173–182.

Azocar, P. C., H. C. Rojo, J. J. Mira, and H. B. Manterola. 1996. Inclusión de nummularia (*Atriplex nummularia* Lindl.) y cladodios de tuna (*Opuntia ficus-indica*) en la dieta de cabras criollas, en reemplazo de heno de alfalfa. 1. Effecto en el consumo, peso vivo y producción de leche. *Avances en Producción Animal* 21: 43–50.

Barbera, G., F. Carimi, and P. Inglese. 1992. Past and pres-

ent role of the Indian-fig prickly-pear (*Opuntia ficus-indica* (L.) Miller, Cactaceae) in the agriculture of Sicily. *Economic Botany* 46: 10–20.

Barbera, G. 1995. History, economic and agro-ecological importance. In *Agro-ecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection paper 132, FAO, Rome. Pp. 1–12.

Ben Salem, H. 1998. Effets de l'*Acacia cyanophylla* Lindl. sur l'ingestion et la digestion des régimes destinés aux ovins. Rôle des tanins et perspectives d'amélioration de sa valeur alimentaire. Ph.D. Thesis, Université de Dijon, Dijon, France.

Ben Salem, H., A. Nefzaoui., H. Abdouli, and E. R. Orskov. 1996a. Effect of increasing level of spineless cactus (*Opuntia ficus-indica* var. *inermis*) on intake and digestion by sheep given straw-based diets. *Animal Science* 62: 293–299.

Ben Salem, H., A. Nefzaoui, and L. Ben Salem. 1996b. Nutritional characterization of some Mediterranean fodder trees and shrubs harvested at different seasons. *Native and Exotic Fodder Shrubs in Arid and Semiarid Zones.* Regional Workshop, Hammamet, Tunisia. P. 23.

Ben Salem, H., A. Nefzaoui, and L. Ben Salem. 1998. Fodder shrubs as supplements to poor quality roughages fed to sheep. *International Symposium "Livestock Production and Climatic Uncertanty in the Mediterranean."* Agadir, Morocco. P. 21.

Ben Salem, H., A. Nefzaoui, and L. Ben Salem. 2000. Supplementing range goats in central Tunisia with feed blocks or a mixture of *Opuntia ficus-indica* var. *inermis* and *Atriplex nummularia.* Effects on behavioural activities and growth. *Proceedings of the 7th International Conference on Goats.* Tours, France. Pp. 988–989.

Ben Salem, H., A. Nefzaoui, and L. Ben Salem. 2002. Supplementation of *Acacia cyanophylla* Lindl. foliage-based diets with barley or shrubs from arid areas (*Opuntia ficus-indica* var. *inermis* and *Atriplex nummularia* L.): Effects on growth and digestibility in lambs. *Animal Feed Science and Technology* (in press).

Ben Thlija, A. 1987. Nutritional value of several Opuntia species. Master's Thesis, Oregon State University, Corvallis.

Brutsh, O. M. 1984. Prickly pear (*Opuntia ficus-indica*) cultivation in Southern Africa. *Symposium of Agricultural Use of the Cactaceae. Prospects and Problems.* International Organization for Succulent Plant Study, Frankfurt.

Castra, J., S. Pérez, and E. Riquelme. 1977. Evaluation of thornless prickly pear silages as a feedstuff for ruminants. *Proceedings Western Section, American Society of Animal Science* 28: 127–128.

Clovis de Andrade, J. 1990. *As Palmas Forrageiras em Alagoas.* Maceio, Alagoas, Brazil.

Cordier, G. 1947. De la composition de quelques produits fourragers tunisiens et de leur valeur pour l'alimentation du mouton. *Annales du Service Botanique et Agronomique de Tunisie* 20: 22–108.

Cottier, H. 1934. Quelques aliments de disette, leur valeur et leur emploi. *La Tunisie Agricole* 37: 127–141.

Curtis, R. J. 1979. Prickly pear farming in the Santa Clara Valley, California. *Economic Botany* 31: 175–179.

De Kock, G. C. 1965. Manejo y utilización del nopal sin espinas. *9o Anales Congreso Internacional de Pasturas,* São Paulo, Brazil, 2: 1471–1474.

De Kock, G. C., and J. D. Aucamp. 1970. *Spineless Cactus. The Farmer's Provision against Drought.* Leaflet No. 37, Agricultural Research Institute of the Karoo Region, Pretoria.

De Kock, G. C. 1980. Cultivation of drought tolerant fodder shrubs. In *Browse in Africa: The Current State of Knowledge* (H. N. Le Houérou, ed.). International Livestock Centre for Africa, Addis Ababa. Pp. 399–410.

De Kock, G. C. 1983. Drought resistant fodder crops. In *Browse in Africa: The Current State of Knowledge* (H. N. Le Houérou, ed.). International Livestock Centre for Africa, Addis-Ababa. Pp. 1–30.

Demeyer, D. I., and C. J. Van Nevel. 1979. Effect of defaunation on the metabolism of rumen micro-organisms. *British Journal of Nutrition* 42: 515–524.

El-Nouty, F. D., G. A. Hassan, T. H. Taher, M. A. Samak, Z. Abo-Elezz, and M. H. Salem. 1988. Water requirements and metabolism in Egyptian Barki and Rahmani sheep and Baladi goats during spring, summer and winter seasons. *Journal of Agricultural Science, Cambridge* 111: 27–34.

Flores Valdez, C. A., and J. R. Aguirre Rivera. 1992. *El Nopal Como Forraje.* Universidad Autónoma Chapingo, Chapingo, Mexico.

Gonzalez, C. L. 1989. Potential of fertilization to improve nutritive value of prickly pear cactus (*Opuntia lind-*

heimeri Engelm.). *Journal of Arid Environments* 16: 87–94.

Gregory, R. A., and P. Felker. 1992. Crude protein and phosphorus contents of eight contrasting *Opuntia* forage clones. *Journal of Arid Environments* 22: 323–331.

Griffiths, D. 1905. *The Prickly Pear and Other Cacti as Food for Livestock.* United States Department of Agriculture Bulletin 74, Washington, D.C.

Harvard-Duclos, B. 1969. *Las Plantas Forrajeras Tropicales.* Blume, Barcelona.

Hoffman, G. O., and A. H. Walker. 1912. *Prickly Pear—Good or Bad?* Texas Agricultural Experiment Station, Bulletin 806, College Station, Texas.

Komisarczuk-Bony, S., and M. Durand. 1991. Effects of minerals on microbial metabolism. In *Rumen Microbial Metabolism and Ruminant Digestion* (J. P. Jouany, ed.). Institut National de la Recherche Agronomique, Paris. Pp. 179–198.

Le Houérou, H. N. 1979. Resources and potential of the native flora for fodder and sown pastures production in the arid and semi-arid zones of North Africa. In *Arid Land Plant Resources* (J. R. Goodin and D. K. Worthington, eds.). ICASALS, Texas Tech University, Lubbock. Pp. 384–401.

Le Houérou, H. N. 1991. Rangeland management in Northern Africa and the Near East: Evolution, trends and development outlook. *Proceedings V International Rangeland Congress,* Montpellier, France. Pp. 543–552.

Le Houérou, H. N. 1992. The role of *Opuntia* cacti in the agricultural development of Mediterranean arid zones. *Proceedings 2nd International Congress on Prickly Pear and Cochineal,* Santiago, Chile. Pp. 186–198.

Lozano, G. M. 1958. Contribución al estudio e industrialización del nopal (Opuntia spp.). Bachelor's Thesis. Universidad Autónoma de Mexico "Antonio Narro," Saltillo.

Metral, J. J. 1965. Les cactacées fourragères dans le Nord Est du Brésil plus particulièrement dans l'état du Ceara. *Agronomie Tropicale* 20: 248–261.

Monjauze, A., and H. N. Le Houérou. 1965. Le rôle des *Opuntia* dans l'économie agricole Nord Africaine. *Bulletin École Nationale Supérieure d'Agriculture de Tunis* 8–9: 85–164.

Nefzaoui, A., and H. Ben Salem. 1996. Nutritive value of diets based on spineless cactus (*Opuntia ficus-indica* var. *inermis*) and Atriplex (*Atriplex nummularia*). *Native and Exotic Fodder Shrubs in Arid and Semi-Arid Zones, Regional Training Workshop.* Hammamet, Tunisia. P. 18.

Nefzaoui, A., and H. Ben Salem. 1998. Spineless cactus: A strategic fodder for West Asia and North Africa arid zones. *International Symposium—Cactus Pear and Nopalitos—Processing and Uses.* Santiago, Chile. Pp. 58–76.

Nefzaoui, A., A. Chermiti, and H. Ben Salem. 1993. Spineless cactus (*Opuntia ficus indica* var. *inermis*) as a supplement for treated straw. *7th Meeting of the FAO Sub-Network on Mediterranean Pastures and Fodder Crops.* Chania, Greece. Pp. 130–133.

Nefzaoui, A., H. Ben Salem, and L. Ben Salem. 1996. La complémentation azotée du cactus inerme pour les ovins. Effet de la source d'azote. *Annales de Zootechuie* 45: 20.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nobel, P. S. 1989. Productivity of desert succulents. *Excelsa* 14: 21–28.

Nobel, P. S. 1994. *Remarkable Agaves and Cacti.* Oxford University Press, New York.

Nordblom, T., and F. Shomo. 1995. *Food and Feed Prospects to 2020 in the West Asia/North Africa Region.* International Center for Agricultural Research in Dry Areas (ICARDA), Aleppo, Syria.

Ørskov, E. R., F. D. Hovell, and F. Mould. 1980. The use of nylon bag technique for the evaluation of feedstuffs. *Tropical Animal Production* 5: 195–213.

Preston, T. R., and R. A. Leng. 1987. *Matching Ruminant Production Systems with Available Resources in the Tropics and Sub-tropics.* Penambul Books, Armidale, Australia.

Rangnekar, D. V. 1988. Availability and intensive utilization of sugar cane by-products. In *Non-Conventional Feed Resources and Fibrous Agricultural Residues* (C. Devendra, ed.). International Development Research Centre and Indian Council of Agricultural Research, Hisar, India. Pp. 76–93.

Roussow, C. de W. 1961. The prickly pear native's fodder bank and silo. *Farming in South Africa* 37: 23–26.

Russell, C. E., and P. Felker. 1987. The prickly pears (*Opuntia* spp. Cactaceae): A source of human and animal food in semiarid regions. *Economic Botany* 41: 433–445.

Satter, L. D., and L. L. Slyter. 1974. Effect of ammonia concentration on rumen microbial protein production *in vitro. British Journal of Nutrition* 32: 199–208.

Silanikove, N. 1992. Effects of water scarcity and hot environments on appetite and digestion in ruminants: A review. *Livestock Production Science* 30: 175–194.

Shoop, M. C., E. J. Alford, and H. F. Mayland. 1977. Plains prickly pear is a good forage for cattle. *Journal of Range Management* 30: 12–16.

Teles, F. F. F. 1978. Nutrient analysis of prickly pear (*Opuntia ficus-indica* Linn.). Ph.D. Thesis, University of Arizona, Tucson.

Terblanche, I. L., A. M. Mulder, and J. W. Rossouw. 1971. The influence of moisture content on the dry matter intake and digestibility of spineless cactus. *Agro-animalia* 3: 73–77.

Theriez, M. 1965. *Recherches sur la Digestibilité de Opuntia ficus-indica var. inermis en Tunisie.* Institut National de la Recherche Agronomique, Tunis, Tunisia.

Tien, V. D., L. V. Ly, N. K. Duong, and B. Ogle. 1993. The prickly pear cactus *(Opuntia elator)* as supplement for sheep in the Phanrang semi-arid area of central region of Vietnam. *National Seminar Workshop on Sustainable Livestock Production on Local Feed Resources.* Hanoi. Pp. 71–74.

Ushida, K., and J. P. Jouany. 1985. Effect of protozoa on rumen protein degradation in sheep. *Reproduction Nutrition Development* 25: 1075–1081.

Valdez, G. C., and V. C. Flores. 1967. *Alimentación del Ganado Lechero Estabulado en al Cd. Saltillo, Coahuila.* Escuela Nacional de Agricultural (Inedito), Chapingo, Mexico.

Viana, S. P. 1965. El uso del nopal sin espinas en la alimentación del ganado. *90 Anales Congreso Internacional de Pasturas.* São Paulo, Brazil. Pp. 1461–1464.

Wehren, W. 1976. Eignung und Futterwert, besonders Aminosäurenzusammensetzung von unkonventionellen Proteinquellen in semi-ariden Gebieten Tunesiens. Ph.D. Thesis, University of Bonn, Bonn, Germany.

Wilson, A.D. 1970. Water economy and food intake of sheep when watered intermittently. *Australian Journal of Agricultural Research* 21: 273–281.

Woodward, T. E., W. F. Turner, and D. Griffith. 1915. Prickly pear feed for dairy cows. *Journal of Agricultural Research* 4: 405–449.

CHAPTER

› 13 ‹

NOPALITOS, MUCILAGE, FIBER, AND COCHINEAL

Carmen Sáenz-Hernández, Joel Corrales-García, and Gildardo Aquino-Pérez

Introduction
Processing of Nopalitos
- *Harvest*
- *Storage*
- *Minimally Processed Nopalitos*
- *Industrial Techniques*

Nopalitos as Products
- *In Brine*
- *Pickled*
- *Sauces, Marmalades, Jams, Candies, and Juices*

Mucilage
Dietary Fiber from Cladodes
Use of Cladodes in Medicine
Cochineal
- *Pre-Colonial and Colonial History*
- *Decline and Resurgence*
- *Importance and Uses*
- *Carminic Acid*

Biology of Cochineal
- *Origin and Diversity*
- *Morphology and Life Cycle*
- *Host*
- *Environmental Factors and Natural Enemies*
- D. coccus *versus Wild Cochineal*

Marketing of Cochineal
- *Production and Prices*
- *Supply and Demand*

Conclusions and Future Prospects
Literature Cited

Introduction

A common use of cactus stems is nopalitos—tender young cladodes—a traditional vegetable eaten fresh or cooked in various dishes. Mexicans are the principal consumers. Nopalitos are generally obtained from *Opuntia ficus-indica, O. robusta,* or *Nopalea* spp. The number of spines and the color are quality factors evaluated by consumers. Several new consumable products are being developed from the stems (e.g., marmalades, blends for breakfasts, and pickles), and the cladodes have medical and cosmetic uses.

Another important use of *Opuntia* stems is the production of carminic acid, a natural colorant developed by the precolonial indigenous people of Mexico. Carminic acid is produced by an insect known as cochineal, or *cochinilla del nopal,* a parasite that infests several species of cacti belonging to two closely related genera, *Opuntia* and *Nopalea.* Identified by the scientific name, *Dactylopius,* the genus has been recognized worldwide since the 16th century as the source of a valuable red pigment, whose main component is carminic acid. Native to the Americas, cochineal was known in colonial times as *nocheztli* or *grana* in New Spain, and as *macno* or *magno* in the Andean region of South America.

The chemical composition of cladodes determines their use as a raw material in the food industry. Cactus stems, as other vegetables, have low protein and fat contents (Table 13.1). The crude fiber is higher than in most other vegetables and is an important consideration for human health. The nitrogen-free extract content is high and includes soluble dietary fiber, insoluble dietary fiber, and some sugars. The ash depends on the soil composition, but the main components are calcium and potassium; sodium and phosphorus are present in lesser amounts. Calcium oxalate crystals, which are insoluble in water, increase with age and can constitute 85% of the ash of old cladodes (Pimienta Barrios 1990; Granados and Castañeda 1991; Sáenz et al. 1997). The crude fiber also increases with cladode age (Table 13.1). This is significant, because young nopalitos can be used as a fresh vegetable in salads, whereas old nopalitos, whose high fiber content makes them difficult to chew, are useful for other purposes. Cladodes have high concentrations of phenylalanine, leucine, and vitamins (retinol and ascorbic acid; Zambrano et al. 1998

Processing of Nopalitos

Nopalitos have formed part of the diet of Mexican people since pre-Hispanic times; nowadays, they are also a specialty vegetable in the United States. Production in Mexico is about 600,000 tons fresh weight per year; under intensive management involving close planting in irrigated and fertilized beds that are often covered with plastic, productivity can be 250 tons ha^{-1} $year^{-1}$ (Flores 1997; Nobel 1998). In Mexico, people prefer to buy thin and turgid cladodes with a fresh appearance and a brilliant green color. They are cooked at home as an ingredient in various recipes for stews, dishes and desserts. Outside Mexico, people of Mexican origin can purchase processed nopalitos. Young cladodes are in a rapid growth phase and have high metabolic activity and high transpiration rates (Cantwell 1991). However, once they are harvested as nopalitos, they have moderate respiration rates (25 microliter CO_2 g^{-1} $hour^{-1}$ at 20°C) and a low ethylene production (0.2 nanoliter g^{-1} $hour^{-1}$ at 20°C; Cantwell et al. 1992). Nopalitos are highly perishable after harvest; the deterioration processes lead to wilting, browning, and microbial contamination by *Alternaria* sp., *Penicillium* sp., and other fungi (Ramayo-Ramirez et al. 1978a), especially when they have been despined and diced.

Harvest

Cladodes for nopalitos are harvested by hand, gripping the bottom of a pad and twisting more than 90° until it snaps off the mother plant. The lower tissues can be torn if this action is not carried out with care, so detached cactus stems and the mother plants can easily be infected by microorganisms. For this reason, cutting a pad at its base with a knife is better than simply twisting it off. In any case, harvested nopalitos must be protected from the sun to lessen metabolism, transpiration, and infection (Corrales 1992a). After harvest, intact nopalitos (with spines) are directly taken to local markets; for distant markets, nopalitos are packed in a shady area.

The form in which nopalitos are transported depends on where the sale takes place and on the distance to the market. The following modalities occur: (1) transportation of intact or despined nopalitos over short distances in vans for sale by bulk in local markets; (2) intact or despined nopalitos, packed in baskets called *colotes* containing approximately 200 pads; (3) 500 to 550 intact nopalitos packed in sacks for the large markets of Mexico City; (4) intact or despined nopalitos packed in cardboard boxes or wooden crates of 10 to 15 kg capacity, when the market is in California or in Mexico near the U.S. border; and (5) intact nopalitos packed in a cylindrical packing unit (*paca*), which is the main mode used for the large markets of Mexico City and other cities in central Mexico (Nobel 1998). The latter packing unit is 1.6 to 1.7 m in height and 0.7 to 0.8 m in diameter, containing 2,500 to 3,000 pads (Corrales 1992a). For a paca, nopalitos are placed horizontally on cloth as a layer inside a metal mold; following its

TABLE 13.1
Chemical composition of cladodes (% of dry matter)

Age (years)	Protein (%)	Fat (%)	Crude fiber (%)	Nitrogen-free extract (%)	Ash (%)
1	5.4	1.29	12.0	63	18.2
2	4.2	1.40	14.5	67	13.2
3	3.7	1.33	17.0	64	14.2
4	2.5	1.67	17.5	64	14.4

Reference: López et al. (1977), cited by Pimienta (1990).

circular form, another nopalito layer is placed upon the first one, and so forth (Corrales-García 1997). Pacas have proved practical, especially when periods of commercialization are short (1–3 days). If the period is longer, considerable heat is generated in the center of the packing units by respiration of the nopalitos (Cantwell 1991), reducing the quality of product.

Storage

Refrigeration atmospheres with reduced O_2 and/or elevated CO_2 concentrations extend the storage life of many fruits and vegetables by reducing respiration rates. However, postharvest deterioration can result from many factors besides high respiration rates, including the biochemical changes associated with respiratory metabolism, ethylene production and action, compositional changes, physiological disorders, and pathological breakdown (Kader 1986). Furthermore, under certain conditions, atmospheric changes shift cladodes from aerobic to anaerobic respiration, leading to fermentation and the accumulation of ethanol and acetaldehyde (Chang et al. 1982) and causing unpleasant flavors and odors.

Storing at low temperatures extends the shelf life of nopalitos and maintains their vitamin content. This is especially true under modified atmospheres, which also implies low O_2 availability for oxidation and browning, low degradation of vitamins, and, in general, low enzymatic activity. Other factors, such as harvest technique, storage duration and relative humidity, and packing technique also affect the shelf life of nopalitos (Cantwell 1995). Ramayo et al. (1978b) found that 21% of pads packed in wooden crates and stored at 10°C (at 80–85% relative humidity) showed decay at the cut surface at 10 days; however, if carefully harvested, the shelf life can be extended to 21 days without decay development under the same storage conditions.

Nopalitos are susceptible to chilling injury when exposed to nonfreezing temperatures below 10°C. This physiological disturbance is typical of some tropical and subtropical fruits and vegetables (Saltveit and Morris 1990; Wang 1990) as well as nopalitos (Ramayo-Ramírez et al. 1978a; Cantwell 1991) and leads to surface discoloration and softening, which, in turn, usually promotes microbial infections. The susceptibility to chilling injury and its consequences vary with species and stem age, the harvest method, and the method of packing as well as with the atmosphere, temperature, relative humidity, and duration of cold storage. Nopalitos of *Opuntia* spp. packed in vented polyethylene bags (leading to a modified atmosphere inside the bag) may show signs of chilling injury at 21 days of storage at 5°C, whereas cactus stems packed in wooden crates and also stored at 5°C show chilling injury at 15 days (Rodríguez-Félix and Villegas-Ochoa 1998). Stems of *Nopalea cochenillifera* are more susceptible to chilling injury during storage at 4°C than are those of *Opuntia* spp. Outside of bags, they develop symptoms of chilling injury at 7 days, but if stored in plastic bags, an additional 4 days of storage is gained before symptoms appear (Nerd et al. 1997).

Minimally Processed Nopalitos

In general, "minimally processed" horticultural products are prepared and handled to maintain their freshness while providing convenience to the consumer. Producing minimally processed products involves cleaning, washing, trimming, coring, slicing, and shredding (Brecht 1995; Schlimme 1995). Other terms used to refer to minimally processed products are "lightly processed," "partially processed," "fresh-processed," and "preprepared" (Cantwell 1992). According to Avena (1996), minimum processing includes the operations generally used for canned, frozen, or dehydrated food products, but without scalding for inactivation of enzymes. Most of these products are sold as ready-to-eat foods, which is a major advantage. "Pre-cut," "minimally processed," or "fresh-cut" can describe a special modality for postharvest handling of fresh nopalitos.

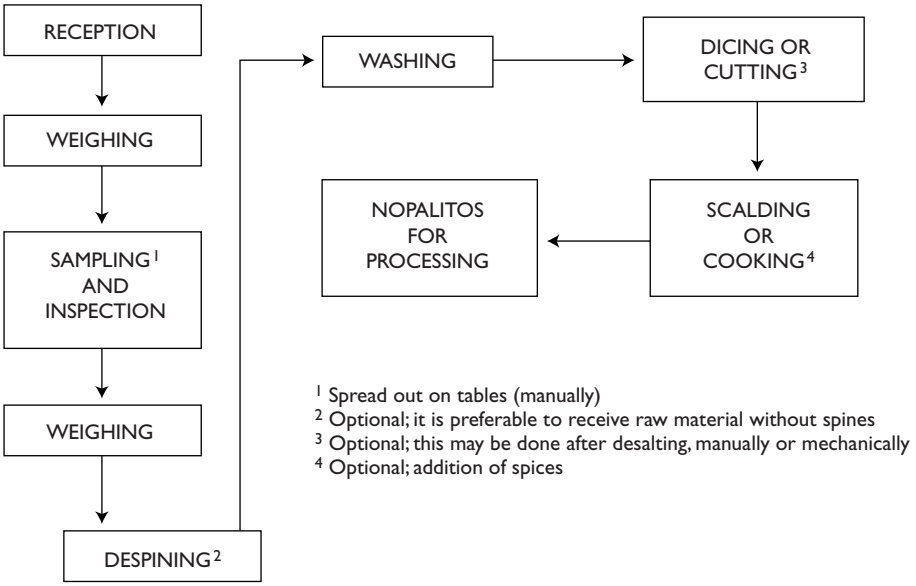

RECEPTION
WEIGHING
SAMPLING [1] AND INSPECTION
WEIGHING
DESPINING [2]
WASHING
DICING OR CUTTING [3]
SCALDING OR COOKING [4]
NOPALITOS FOR PROCESSING
[1] Spread out on tables (manually)
[2] Optional; it is preferable to receive raw material without spines
[3] Optional; this may be done after desalting, manually or mechanically
[4] Optional; addition of spices

Figure 13.1. Flow diagram for conditioning raw nopalitos for later processes. Adapted from Corrales-García (1998).

Cleaning and despining of nopalitos—the latter an obligatory postharvest practice for nopalitos—is usually done at the destination market just before the retail sale. This practice is generally carried out using a knife by people with highly developed skill. Nowadays, diced pads, whose spines have been removed, are packed in plastic bags and sold in Mexico and the southwestern United States.

Nopalitos whose spines have been cut off have higher metabolic activity and transpiration rates than do intact nopalitos. Also, mucilage leaking, wilting, and oxidation occur quickly, and their shelf life is short. For these reasons, despined and diced nopalitos are more perishable than is the intact product. In general, the main problems that limit shelf life of minimally processed nopalitos are brown discoloration at the cut surfaces (caused by polyphenol oxidases), mucilage leakage (undesirable mucilage accumulation inside the bag, which increases with dicing), unpleasant flavor caused by accumulation of anaerobic metabolites, and a surface yellowing, which leads to a color change from brilliant green to brownish green and gives them a cooked appearance. Vacuum packing of diced pads does not increase the shelf life at refrigerated storage temperatures (Rodríguez-Félix and Soto-Váldez 1992). Also, the type of packaging, the storage temperature, and the local atmosphere affect storage of minimally processed nopalitos. For instance, 4°C is better than 10°C for storage up to 15 days, and polypropylene (25 µm thick) is better than polyethylene (35 µm thick).

Industrial Techniques

Many alternatives for processing cladodes, nopalitos, and tuna fruits have been described (Colin 1976; Corrales 1992b; Sáenz 1995). Industrially processed nopalitos can last longer than fresh ones, allowing sales in distant markets. Also, the supply can be extended to other months, and prices and quality can be controlled. The variety of products obtained by industrialization adds value to the product and makes diversification of markets possible. Industrialization also generates rural employment, which contributes income that benefits the producer communities (Corrales 1992b). Today in Mexico some companies process nopalitos mainly for export, because domestic consumers prefer to buy fresh nopalitos and then cook them at home.

The first steps in industrial processing of nopalitos are reception and conditioning of the raw material, which should be of the highest quality and be despined by the grower (Fig. 13.1). Conditioning consists of scalding and washing. Scalding deactivates enzymes, destroys microorganisms, softens the tissues, and partially eliminates the mucilage. The main variables are temperature and duration of scalding, as well as additives that improve the product. Nopalitos of the wild nopal 'Tapón' (*Opuntia robusta*) lend themselves to higher temperature and longer cooking time than do cultivated nopalitos, such as the variety 'Milpa Alta' (*Opuntia ficus-indica*). The final product is washed with cold clean water, which fixes the characteristic green



Figure 13.2. Various brands and preparations of processed nopalitos available in Mexico as collected by the Programa Nopal (Cactus Pear Program) of Centro de Investigaciones Económicas, Sociales y Tecnológicas de la Agroindustria y la Agricultura Mundial (CIESTAAM), Universidad Autónoma Chapingo, México.

color of nopalitos and eliminates adhering pectins and mucilage (Corrales-García 1998). The resulting nopalitos can be used for various products, e.g., nopalitos in brine, pickled nopalitos, and marmalades.

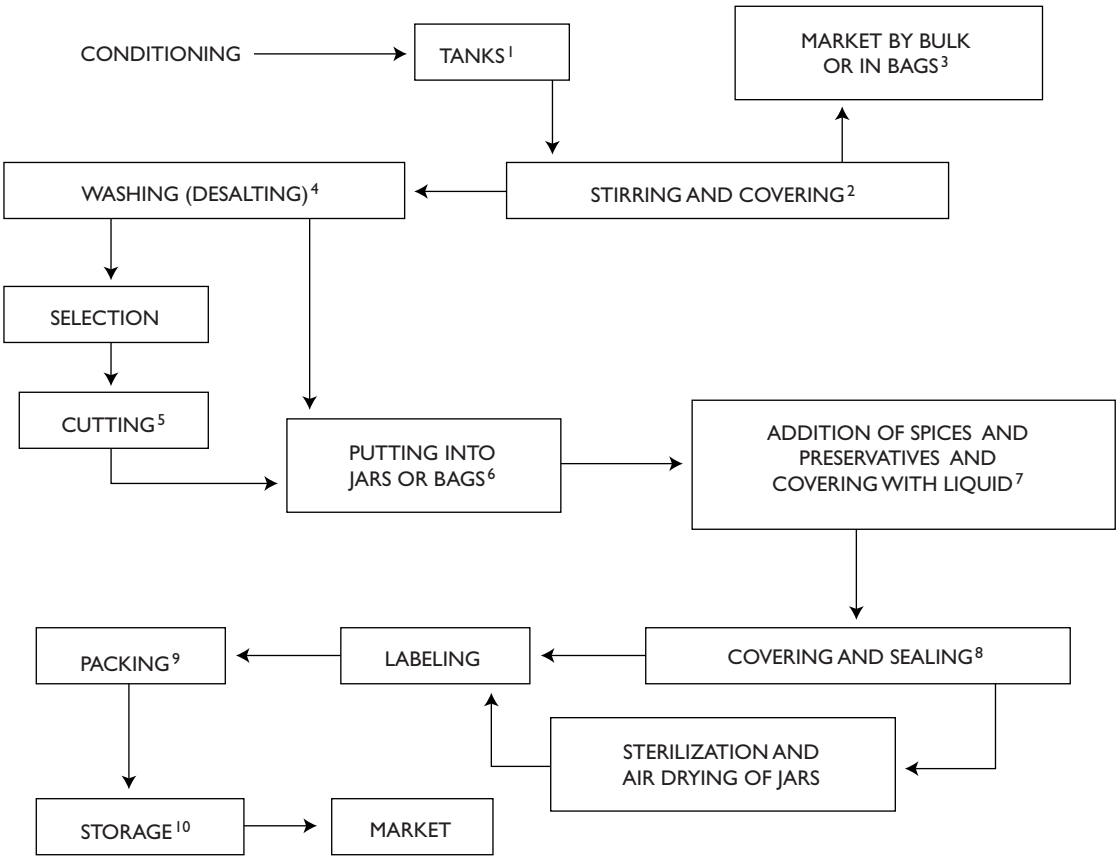
Nopalitos as Products

In Brine

Nopalitos can be preserved in a saline solution (maximum 2% NaCl) and then canned, placed in plastic bags, or packed in glass or plastic jars to be used later to prepare various Mexican foods. More than 20 brands are currently available in Mexico (Fig. 13.2), many with their own preparation process. The conditioned nopalitos (Fig. 13.1) are commonly salted in large tanks containing 12% NaCl brine, using approximately 1.7 liters of brine for each kilogram of nopalitos (Fig 13.3). Nopalitos must remain in these tanks for at least 10 days and can be kept there for months. The high concentration of salt extracts water from the nopalitos, so salt must be added to maintain the brine. The tanks should be stirred daily with a wooden paddle. Also, the tanks should be covered to avoid contamination and discoloration of the product by light.

When salting is finished, the product is taken to the process room, where it is desalted by washings (Fig. 13.3). Later, it is sorted, diced, and canned, or put into plastic bags or jars with a few spices and covered with 2% brine. The bags are sealed; the cans or jars are evacuated, covered, and sterilized in an autoclave or water-bath, then left to air dry before labeling. Bags, cans, or jars are packed in cardboard boxes and stored for the quarantine period; eventually they are shipped to the market. The product can also be sold in bulk without desalting (Fig. 13.3).

Compared with intact nopalitos (with spines), the final yield of nopalitos in brine ready for sale is about 57%, depending on the process and its control. The following procedures can improve success: (1) implement a well-defined program and rigorous quality control beginning with the reception of the raw material—e.g., remove pads that are bruised or flawed; (2) implement a quarantine program that maintains the product's quality for as long as possible; (3) avoid direct contact of the brine with a reactive metal (such



[1] 12% brine
[2] Daily stirring with wooden paddle
[3] In wooden or plastic containers
[4] During approximately 6 hours, until reaching 1-2% salt
[5] Optional: manual or mechanical
[6] In plastic bags or glass or plastic jars
[7] 2% brine
[8] Brine must cover nopalitos completely (to avoid air reaching the pads)
[9] In cardboard boxes
[10] Quarantine

Figure 13.3. Flow diagram for processing nopalitos in brine. Adapted from Corrales-García (1998).

as unpainted iron); (4) maintain the brine at a minimum NaCl concentration of 10% that is verified constantly with a special salt meter, and stir daily to help ensure uniform salinity; (5) completely cover the nopalitos with brine (weigh them down with a plastic or wooden screen); and (6) because light and extraneous material (e.g., dust, dirt, litter, water, insects) are detrimental, cover the tanks.

Pickled

Pickled nopalitos consist of scalded nopalitos preserved in vinegar (maximum 2% of acetic acid) with spices and vegetable seasonings (García 1993). More than 25 companies in Mexico currently pickle nopalitos, and many have their own preparation processes (Fig. 13.2). The conditioned nopalitos (Fig. 13.1) are cut or diced (manually or mechanically; Fig. 13.4). Pickling is done with vinegar (1.9–2.0% acetic acid), spices, aromatic herbs, and olive oil. The vinegar is heated to boiling, and then the spices are added, either directly or in a cloth bag. The mixture is boiled for 5 minutes to allow the vinegar to absorb the aromas. Separately, onion slices, garlic cloves, laurel leaves, and carrot discs are lightly fried in vegetable oil. Then the nopalitos, vinegar, and sautéed vegetables are mixed. This mixture is canned, or put into plastic bags or jars. The bags are sealed, and the cans and jars are evacuated and covered; they are then sterilized in an autoclave or in a water-bath.

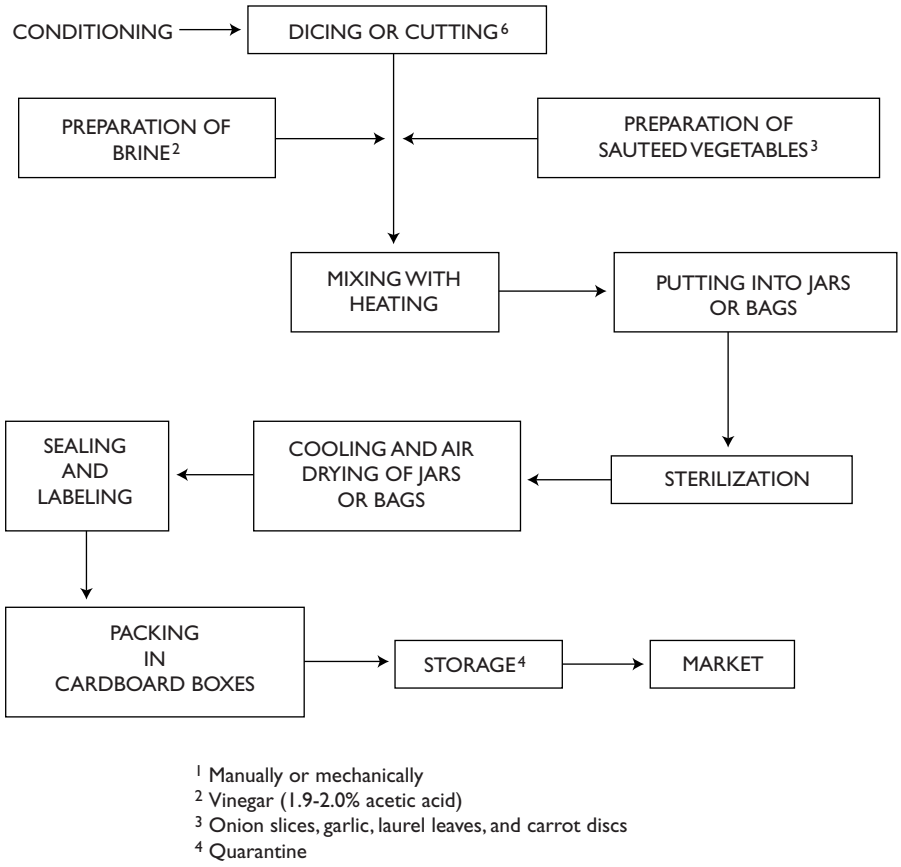


Figure 13.4. Flow diagram of production process for pickled nopalitos. Adapted from Corrales-García (1998).

Finally, they are left to air dry before labeling. Bags, cans, or jars are packed in cardboard boxes, stored for the quarantine period, and then shipped to the market.

Sauces, Marmalades, Jams, Candies, and Juices

Nopalito sauces are prepared using milled nopalitos, with addition of various chilis, tomato, onions, vinegar, and spices (in different proportions), and, often, a preservative. More than 15 brands of nopalito sauce occur, some with white wine or lemon concentrate. The sauces can have whole pieces of nopalito or be totally milled, depending on the market preference. In Mexico, nopalito sauces are generally prepared daily using fresh ingredients, rather than as canned sauces for the market. In addition to sauces, recently in Mexico nopalitos are incorporated into sausages using soybean flour, and nopalitos are prepared with tuna fish, beans, jalapeño chilis, and mushrooms. These products are prepared by large, established companies, following principles of modern food technology.

Another product from nopalitos is marmalade. This product is prepared using milled nopalitos cooked with various concentrations of sugar, pectin, and preservatives. The conditioned (scalded) nopalitos (Fig. 13.1) are chopped (manually or mechanically) and cooked for a second time. Tirado (1986) made a jam with cladodes, adding orange juice, peel, and sugar in the ratio of 1:1.5:0.8:0.8. The jam had no microbial growth after 40 days of storage. This product is similar to other jams in the Mexican market (e.g., fig and orange) with respect to aroma, color, taste, texture, and appearance.

Badillo (1987) made a jam using cladodes, sugar, and citric acid, obtaining a product with good sensory quality and microbiological stability. Sáenz et al. (1995a) made a marmalade from cladodes after treating with 2% $Ca(OH)_2$ to lower the mucilage content (which causes texture and acceptability problems). Lemon juice and lemon peel were included; the first lowered the pH and the second, together with pectin, aided the gelling of the product (67°Brix, 0.97% acidity, and good acceptability). About six companies in Mexico and the United States presently

manufacture marmalades. Mucilage obtained by milling and filtrating nopalitos can lead to better consistency in marmalades of other fruits (e.g., blueberry, raspberry, blackberry, strawberry, peach, apple, pear, pineapple, and plum), and therefore has potential to expand the world market for nopalito products.

Candies made with nopalitos are processed with sugar and often various other ingredients. The main confectionary products include crystallized nopalitos, nopalitos in syrup, nopalito candies covered with chocolate, marshmallows with nopalito mucilage (*gomitas*), candies of nuts cooked with honey and platyopuntia mucilage. Villareal (1996) studied the manufacture of crystallized cladodes, which are similar to crystallized melon peel. Sucrose or sugar-cane syrup can be used, and the candies are especially enjoyed by children. The cladodes are cut into pieces that are 1.8 × 4.0 cm, treated with $Ca(OH)_2$ (to remove the mucilage), washed, osmotically dehydrated with a high concentration sucrose solution, and further dehydrated in a forced-draft oven at 60°C. The final product has an intermediate moisture content and can be covered with sweet or bitter chocolate to be more attractive to consumers.

Rodríguez (1999) developed a nopal juice using young pads by scalding, milling, and filtering, then adding citric acid and aspartate. The juice was put in bottles, pasteurized, and vacuum sealed. The product has a pleasant sweet taste, brilliant green color, only 10 calories per bottle, and 10% nopal pulp. A mixed juice of nopal and guava is being marketed nationally and internationally by a Mexican company. Despined and diced nopalitos are milled in a blender with water, the thick juice is filtered to separate solids, the filtered juice is mixed with guava juice, and finally the mixture is pasteurized and bottled. The world market for fruit and vegetable juices has expanded, so nopal juices, mainly in mixtures with other fruits, offer great possibilities for development.

Mucilage

The complex polysaccharide mucilage is an important component of platyopuntias. Mucilage has great potential as part of dietary fiber and also imbibes large amounts of water, forming viscous or gelatinous colloids (Amin et al. 1970; McGarvie and Parolis 1979a,b, 1981; Paulsen and Lund 1979; Trachtenberg and Mayer 1981; Sáenz et al. 1992). Mucilage is composed of varying proportions of L-arabinose, D-galactose, L-rhamnose, D-xylose, and galacturonic acid, the latter representing 18 to 25% of the residues, depending on whether the mucilage comes from fruit or cladodes (Sáenz 1995). The primary molecular structure is a linear chain containing galacturonic acid, rhamnose and galactose, to which xylose and arabinose residues are attached in peripheral positions.

Mucilage can be used as a thickening agent in foods and pharmaceutical products. Sáenz et al. (1992) showed that increasing the pH from 2.6 to 6.6 increased the viscosity of water dispersions of mucilage from 37 to 58 centipoise (37–58 mPa s). Cárdenas and Goicoolea (1997) and Cárdenas et al. (1997) studied the rheological properties of mucilage of different concentrations (0.4 to 6%) with NaCl (0.1 M) and report that the non-Newtonian shearing behavior is similar to that of okra mucilage solutions. In particular, with increasing mucilage concentration a strong tendency occurs for aggregation. Nobel et al. (1992) report that the mucilage content of cacti varies with species and is influenced by irrigation and temperature. For instance, for four sympatric cacti from the Sonoran Desert, mucilage is absent from *Ferocactus acanthodes,* is 19% of the dry weight for *Opuntia basilaris,* 26% for *O. acanthocarpa,* and 35% for *Echinocereus engelmannii;* L-arabinose varied from 17 to 51% of the sugar monomers. For *Opuntia ficus-indica* mucilage in the cladodes increases 24% as the day/night air temperatures during growth are reduced from 30/20°C to 10/0°C (Goldstein and Nobel 1991). For the widely occurring, cold-hardy *Opuntia humifusa,* mucilage in the stems approximately doubles when plants growing at day/night air temperatures of 25/15°C are transferred to 5/–5°C for 7 weeks (Loik and Nobel 1991).

With regard to special applications, farmers in Chile and some other countries use cactus mucilage to clarify drinking water. As for other water-soluble polymers, mucilage flocculates sediment particles and precipitates them out of solution (B. Crabb, personal communication). Another traditional use by the farmers in Chile is to take advantage of the adhesive properties of mucilage to improve external paint; chopped cladodes are blended with lime (mostly $Ca[OH]_2$) and applied to the external walls of houses. Cladode mucilage has also been used for a long time as a glue in combination with lime plaster in Mexico. Mucilage helps the lime to set more quickly and improves the water repellency. This plaster is traditionally used over both earthen (adobe) and brick walls and also as a breathing water-barrier in stucco. Gardiner et al. (1999) found that a cladode extract improves water infiltration in soils, similar to the effects of polyacrylamides. Cactus mucilage also has culinary uses, such as a fat replacer and a flavor binder (J. McCarthy, cited in Cárdenas et al. 1997).

Dietary Fiber from Cladodes

The market in developed countries is increasing for healthful foods with low calories, low cholesterol, low fat, and a

high fiber content. Studies showing the relation among fiber consumption and control of cholesterol as well as the prevention or treatment of some illnesses, such as diabetes, obesity, gastrointestinal disorders associated with a lack of dietary fiber intake, and even colon cancer (Sloan 1994; Grijspaardt-Vink 1996; Hollingsworth 1996), have helped to promote this market. Dietary fiber is composed of several chemical components that are resistant to digestive enzymes, e.g., cellulose, hemicellulose, pectin, lignin, and gums (Spiller 1992; Periago et al. 1993). The fiber content of a food varies with the plant species and the stage of maturity, but seeds, berries, fruit skins, and the bran layers of cereal grains generally contain a large amount of fiber. Based on water solubility, soluble dietary fiber is contributed by mucilage, gums, pectin, and some hemicelluloses, and insoluble dietary fiber by cellulose, lignin, and most hemicelluloses (Periago et al. 1993). Nopal cladodes (i.e., nopalitos) are a good source of dietary fiber.

Sepulveda et al. (1995) obtained a natural concentrate of nopal fiber ("nopal flour") using 2- to 3-year-old cladodes obtained from pruning. Sáenz et al. (1997) and Sáenz (1998) studied the dietary fiber content and some physical and chemical characteristics of this concentrate, as well as the effect of concentration (2.5, 5.0, and 7.0%), temperature, and pH on the viscosity. Viscosity of nopal flour suspensions is an important parameter when the nopal flour is mixed with other food ingredients; the pH also affects such suitability (Lecaros 1997). Nopal flour consists of 43% total dietary fiber, of which 28% is insoluble and 15% is soluble. Rosado and Díaz (1995) reported a dietary fiber content in dehydrated nopal of 50%, indicating that the type of *Opuntia,* the climatic conditions, irrigation, and/or the age of the cladodes can influence the dietary fiber. The water-holding capacity in the former case is 5.6 g per g dry mass, and in the latter case is 11.1 g g^{-1} dry mass for cladodes and 7.1 g g^{-1} for a nopal isolate. The water content indicates the physiological status of the fiber, as water absorption increases the bolus and produces a satiation effect. The water absorption ability depends mainly on particle size and can be modified by controlling the milling process: the smaller the size of the particles, the greater the water retention, as for wheat bran flour.

Nopal flour is being tested for various foods, such as vegetable soup and a gelled dessert (Albornoz 1998; Vallejos 1999). The percentage of added flour is limited: greater than 20% affects the texture of the product. Sáenz et al. (1995b) and Fontanot (1999) tested different replacement proportions of wheat flour by nopal flour in biscuits; more than 15% replacement affects the texture and sensory characteristics of the biscuits but increases the dietary fiber content. Recently, a dehydrated pelletlike product made from dehydrated cladodes has appeared in the Mexican market. This product, which is a blend of wheat fiber, nopal fiber, salt, and the sweetener aspartame, is similar to a common breakfast cereal and is recommended to help control obesity.

Use of Cladodes in Medicine

According to popular medicine, mainly in Mexico, many diseases can be fought and cured with the cladodes, fruit, or other parts of cacti, such as the flowers (Hegwood 1990; Pimienta Barrios 1990; Barbera 1991; Mulas 1993). Nevertheless, only a few applications have a strong scientific basis, such as their effect on diabetes mellitus, blood glucose levels, hyperlipidemy (excess of lipids in the blood), and obesity (Gulías and Robles 1989).

Frati-Munari et al. (1990) studied the hypoglycemic effect of cladodes of *Opuntia ficus-indica,* concluding that glycemia decreased in all patients tested following ingestion and reached statistically significant lower levels after 3 hours; Ibañez-Camacho et al. (1983) confirmed this hypoglycemic action. Ramírez and Aguilar (1995) in a meta-analysis conclude that *Opuntia* has a strong glucose reduction effect. Trejo et al. (1995) evaluated the hypoglycemic activity of a purified extract from platyopuntias on STZ-induced diabetic rats; although the mechanism of action is unknown, the magnitude of the glucose control by the small amount of *Opuntia* extract required (1 mg per kg body weight per day) precludes a predominant role for dietary fiber. Hernández et al. (1997, 1998) used Wistar rats to compare the effect on weight loss of the consumption of nopal fiber and other vegetable fibers, such as cellulose and corn peel fiber. The nopal fiber produces more feces than the other fibers, although all rats lost weight during the study.

Frati-Munari et al. (1992) evaluated the role of commercial capsules (Fig. 13.5) containing dried and ground cladodes in the management of diabetes mellitus. Thirty capsules, each containing 335 mg of dried cladodes, were given to diabetic subjects, and serum glucose was measured throughout 3 hours; the control was performed with 30 placebo capsules. The dried cladodes did not show a hypoglycemic effect and did not influence the glucose tolerance test. In diabetic patients, serum glucose, cholesterol, and triglycerides levels did not change with ingestion of *Opuntia* cladodes. In healthy individuals, glycemia did not change with cladode ingestion, whereas cholesterol and triacylglycerides decreased. Fernández et al. (1990) found effects of platyopuntia cladodes on low-density lipoproteins, suggesting that an extract may decrease cholesterol levels

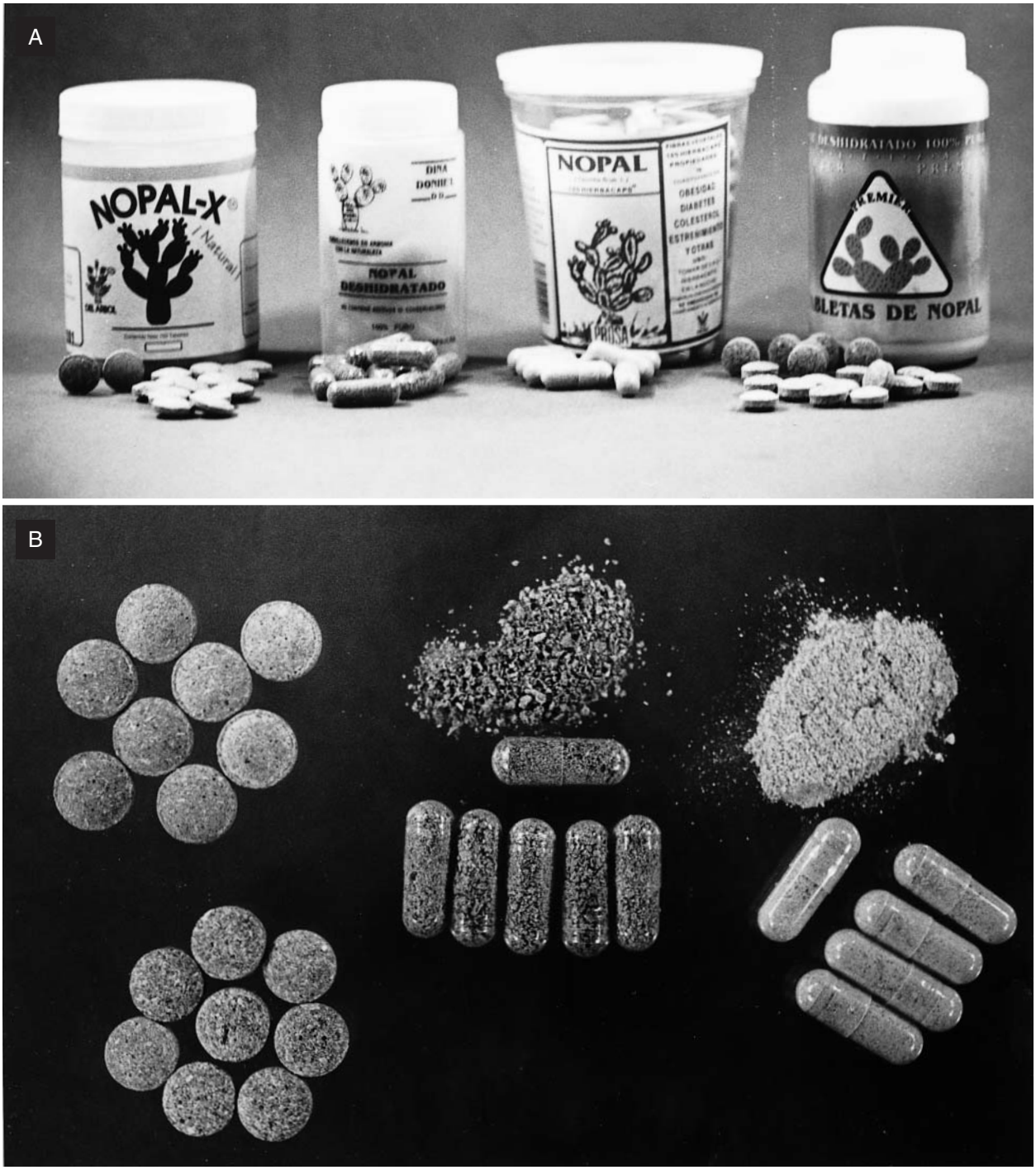


Figure 13.5. Capsules and tablets prepared from dried *Opuntia* cladodes in Mexico: (A) packaging and (B) contents.



Figure 13.6. Various brands and preparations of *Opuntia* cladode extracts used cosmetically in Mexico, as collected by CIESTAAM (see Fig. 13.2.).

More than 30 brands of powders, capsules, and tablets made of dried platyopuntia cladodes are produced in Mexico as nutritious complements (Fig. 13.5). Powder is prepared from cladodes (1.5–2.5 years old) that are washed (chlorinated water), despined, cut, and then dehydrated (at 35–40°C), preferably with forced air. They are then milled and screened, until a fine powder is obtained. This powder is sold in bulk or encapsulated, or it is added with an agglutinant and then compressed to obtain tablets (Frati-Munari et al. 1992; Sepúlveda et al. 1995). Such products are marketed by promoting their alleged medicinal effects, and consumers consume them as medications. Indeed, cladode-derived products are sold for the control of diabetes, cholesterol, gastric and intestinal afflictions, and obesity. This utilization is due to three main factors: (1) the existence of customs, traditions, and pre-Hispanic knowledge of medicine and the traditional herbalists of Mesoamerica (cladodes can cure renal illnesses and erysipelas, induce childbirth, alleviate pain, and heal wounds); (2) various medical studies indicating that the consumption (ingestion) of raw, boiled, roasted, or stewed cladodes decreases glucose and cholesterol in blood in healthy and certain diabetic people, but not in insulin-dependent animals or humans (Ibañez-Camacho and Roman 1979; Ibañez et al. 1983; Fernández et al. 1990; Meckes and Roman-Ramos 1986; Frati-Munari et al. 1989; Trejo et al. 1991); and (3) a modern trend toward "natural" product consumption.

The production of cladode products as over-the-counter medicinal products is growing fast. Frequently, these products have scientifically unfounded claims as to their healing properties. Currently, 21 companies in Mexico produce capsules, 15 produce tablets, and five produce powders (Fig. 13.5). Some of these companies export their products to the United States as nutritious complements. The hypoglycemic effects that many of these products purport to have is unproved (Frati-Munari et al. 1992). At least 30 capsules may need to be consumed per day, which is not comfortable for the patients.

Cosmetics (Fig. 13.6) incorporating cladodes are used for hygienic purposes to beautify the skin and the hair, in accordance with the herbalists of Mesoamerica and popular as well as traditional knowledge. In Mexico more than 20 companies manufacture more than 40 different cosmetic products with platyopuntias, adding portions of juice of the cladodes in their formulations. These products, being of "natural" origin, are increasingly accepted in

Mexico and the United States. However, the cosmetics industry does not require large quantities of cladodes, because they are only a small ingredient in the formulations of these products. The principal cosmetic products (Fig. 13.6) are: (1) shampoos, conditioners, and gels for the hair; (2) soaps; (3) creams as well as facial masks to reconstitute, moisten, clean, or strengthen the skin; and (4) astringent or absorbent lotions (to reduce epidermal fat).

Cochineal

Two types of cochineal, the dye-producing cactus parasite, are recognized. They are classified according to the quality and concentration of their pigments, as well as their biological and morphological characteristics: (1) fine cochineal (*Dactylopius coccus* Costa), and (2) wild cottony cochineal, comprising a group of eight species. Though a noxious pest in nopal fruit orchards, wild cochineal is beneficial as a biological control of weedy nopal infestations throughout the world. Both *D. coccus* and cottony cochineal are easily propagated in various microclimates of North and South America. Although Mexico's central, southern, and southeastern highlands harbor a great diversity of both *Opuntia* and *Dactylopius* and the Mesoamerican region has the oldest records of systematic exploitation of cochineal, Mexico is presently not a major commercial producer of cochineal. The Andean region of South America, noteworthy for having the oldest evidence of cochineal use, currently accounts for 95% of world production. Use of the dye has spread to all nations except several Middle Eastern and Asian countries. Cochineal depends on platyopuntias for its propagation and survival, making its role as host one of the most important uses of *Opuntia.* Therefore, until technological development obviates the need of a host in the cultivation of cochineal, platyopuntias will be a determining factor in the production of the dye insect.

Pre-Colonial and Colonial History

Archaeological evidence for the use of cochineal exists in prehistoric textiles recovered from the Nazca (Classic) and Chimu (Postclassic) cultures of Peru. Saltzman (1992) reports incipient use of *Dactylopius* around the time of Christ and increased utilization in woolen textiles from the late Classic period (7th century). By the 10th century, cochineal was in common use. The first historical reports of cochineal from Peru date from 1533 (Donkin 1977). Evidence of pre-Hispanic cochineal use in Mexico is surprisingly scarce; only a few fragments of pre-Conquest cochineal-dyed fabrics have been found (Donkin 1977). Nevertheless, cochineal was a tribute item in Aztec and Inca empires, in the form of richly colored woolen and cotton mantles (Donkin 1977) and in dye taxed by the Aztec governors. Two basic forms were used: (1) dried cochineal, and (2) cakes or tablets (*panes, pastillas*), known as *nochezt-laxcalli* in Nahuatl, produced by the Indians from the dried, milled insect, leaves of the *tezhoatl* tree, and alum (Dahlgren 1963; Donkin 1977). In contrast to wool, cotton is difficult to dye with cochineal alone. To make the color bind and become permanent, a mordant is required, and alum was used for this in both Mexico and South America. De Sahagún (1829) reported that alum (*tlaxocotl*) was well known in Mexico; other additives were also used as reinforcing agents with cochineal or to vary the shades of red (Donkin 1977).

Cochineal was also used as a paint for articles ranging from houses (Zoque Indians in Chiapas) to the famous Mixtec codices. It was employed by Indian women as a cosmetic, and possibly had pharmaceutical and culinary uses (Dahlgren 1963; Brana 1964; Donkin 1977). Cochineal and silk production flourished in New Spain during the 16th century, although competition occurred between the two insect cultures, particularly in the Mixteca Alta region of Oaxaca. Main producing areas continued to be Oaxaca and Puebla, and at the urging of governor Gómez de Cervantes, Tlaxcala became an important producer. Before 1600, proposals for a royal monopoly of cochineal production in New Spain were circulating. Production in Tlaxcala and Puebla, however, dropped in the mid-17th century. After 1650, Oaxaca was described as the main supplier, and, by the end of the 18th century, Oaxaca was the only significant producer of fine cochineal (Donkin 1977).

Decline and Resurgence

In the 1860s, the introduction of aniline dyes, stronger and faster binding than cochineal, apparently sounded the death knell for the insect dye. France, in 1860, and soon thereafter, the United States, authorized the use of synthetic colorants in foods. In the early 1880s, mineral colorants, including lead-based pigments, began to be used in foods and cosmetics. However, toward the end of the 19th century, medical problems arising from dye use began to be detected. For this reason, in the late 1890s and early 1900s, several European countries, including Italy, Germany, France, and Belgium, as well as Australia and the United States, promulgated regulations for the control and use of certain colorants in food. During 1950 to 1980, various synthetic colorants were decertified. As a result of these prohibitions, interest in natural colorants was renewed. The natural red dyes belonging to three pigment groups (carminic acid, anthocyanin, and betalains) were allowed

to bypass the certification process by the United States Federal Drug Administration Agency (von Elbe 1977).

In 1974 possible toxicological effects of cochineal carmine were reported. In response, the Joint FAO/WHO Expert Committee on Food Additives demanded testing of the colorant for toxicity, and urged lower levels in food products. In 1976, the use of carmine was only permitted in alcoholic beverages and only for a limited time, thus precipitating a price drop for cochineal and carmine. At the request of Peru, the principal producer country, and of the FAO/WHO, the British Industrial Biological Research Association (BIBRA) undertook a series of investigations to determine effects of carmine in food and cosmetics. Several studies were undertaken in 1980 through 1982, including tests of teratogenicity and embryotoxicity as well as effects on multigenerational reproduction in rats (Ford et al. 1987; Grant and Gaunt 1987; Grant et al. 1987). On the basis of these results, in 1982 the FAO/WHO renewed authorization of carmine and its derivatives. Certain imprecision in the BIBRA studies, as well as cases of reactions to carmine in persons with allergies, have led to more recent studies with contradictory results: adverse effects were reported by Quirce et al. (1994), whereas innocuousness was indicated by Kawasaki et al. (1994) and many others. The pros and cons of carmine use have had a significant impact on the prices of this pigment in the world market.

Importance and Uses

The main coloring element of cochineal is carminic acid (Fig. 13.7); secondary elements include kermesic and flavokermesic acid (Wouters 1990) and minor pigments (Sugimoto et al. 1998). Carminic acid is used today in the industrial production of cosmetics, food, and medicines, as well as in textile and other dyeing, although azo synthetic dyes have, to a great extent, replaced the natural dyes in the latter two categories. Tütem et al. (1996) have also reported possible therapeutic uses. Moreover, cochineal, in powdered form, is utilized in food products and especially in the dyeing of textiles in countries such as Iran and Iraq and, in Mexico, among the Zapotec Indians (Ross 1986). Color and hue in textiles depend upon the mineral salts or reagents with which the powder is mixed (Avila and Remond 1986).

As an aqueous or alcohol extract, cochineal is an important colorant in food and beverages; as carmine, it is of importance in cosmetology, medicine, and food products. Carmine is marketed in a number of commercial presentations, including carminic acid at 90% (used as a colorant in processed food products and soft drinks) and lakes (purplish red pigments) composed of carminic acid at concentrations of 40 to 65% combined with a variety of inorganic carriers, of which aluminum and calcium are the most common. Carmine 50 is the most sought-after commercially, e.g., as an additive to acidic beverages.

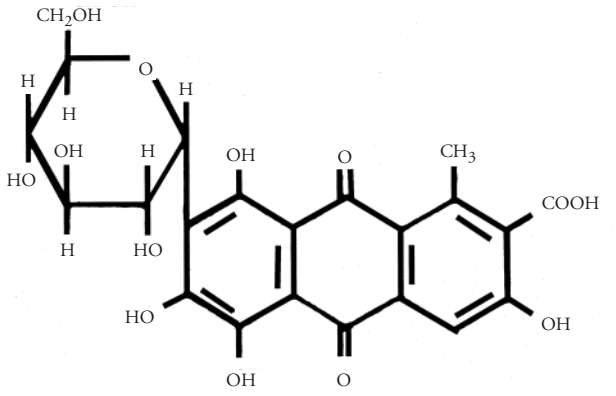


Figure 13.7. Structure of carminic acid.

Carminic Acid

The physical and chemical properties of carminic acid were studied by Lieberman and his associates in 1909 and by Dimroth and colleagues from 1909 to 1920. The molecular structure of carmine was first proposed by Miyagawa and Justin-Mueller in 1920s, with further evidence provided by Fieser and Fieser in 1944 and by Hay and Haynes in 1956 and 1958 (Ali and Haynes 1959). Carminic acid is a hydroxyanthraquinone linked to a glycosyl group (Fig. 13.7). Lac dye and kermesic acid (Old-World insect-derived red dyes) have the same basic chemical structure but without the glycosyl linkage. Glycosyls apparently enhance the intensity of the anthraquinone group in the visible part of the spectrum. The chemical formula of carminic acid is 7β-D-glucopyranosyl-9,10-dihydro-3,5,6,8-tetrahydroxy-1-methyl-9,10- dioxo-2 anthracene carboxylic acid (Fiecchi et al. 1981). The colorant is listed in the *Chemical Index* as Natural red 75470. Carmine is an aluminum chelate of this molecule at a rate of 1:2 aluminum:carminic acid. The great resistance of carminic acid to hydrolysis is due to the glucosyl group. According to Hay and Haynes (1956, 1958; cited in Ali and Haynes 1959), the glucosyl can be D-arabinose, which lends it a pink color, or glucose, which provides a yellow color. There are many commercial products on the market, so chemical and physical properties are asssigned by the firms. Carminic acid precipitates from alkaline solutions as prism-shaped crystals, obliquely truncated and red; they turn reddish-orange in the presence of light. The *Merck Index* describes their characteristics as:

(1) no distinct melting point; (2) darken at 120°C; and (3) deep red color in water and yellow to violet in acid solutions.

For the fabrication of carmine and its derivatives, Avila and Remond (1986) review 12 of the many extraction and purification techniques commonly employed. All techniques follow the principles established by De la Rue, Lieberman, Dimroth, and others. In particular, the processing steps are: (1) separation of fats; (2) extraction of the coloring agent by steeping in a solvent; (3) salt precipitation, which also varies according to the technique employed; and (4) separation, washing, concentration, and drying of the final product. ITINTEC (1990) published a detailed methodology to obtain a carmine extract with a carminic acid content of 62 to 64%: (1) cleaning of insect using a screen; (2) separation of fats with hexane; (3) milling; (4) water extraction (100°C for 10 minutes) adding sodium carbonate until the pH is 9.0; (5) screening and filtering; (6) precipitation (aluminum and calcium salts, 100°C for 15 minutes); (7) pH modification (4.8–5.4); (8) decanting for 2 hours; (9) centrifuging or press filtering; (10) washing with deionized water; (11) drying (40°C) to achieve a water content of 7 to 10%; and (12) packaging in polyethylene bags. Acetone can be used for the separation of fats, an ethanol-water solution for their extraction, and a concentration operation done before filtration (Pérez 1992). To obtain essentially pure carminic acid (99.5%), the main operation is crystalization, beginning with a supersaturated solution.

The extraction of dye from the insect is generally made without any other aid but pure water (J. A. Bustamante, personal communication). The water should be near boiling, and the dye is extracted from dried insects using two or three extractions (70:1 H_2O:cochineal). The resulting fluid is filtered, usually through a press filter, to obtain a solid-free extract (the pH is often reduced to 4.5 with hydrochloric acid). The carminic dye solution can either be spray-dried or laked with aluminum-calcium salts in the presence of citric acid at a high temperature, and then allowed to cool and precipitate in the form of insoluble, bright-red carmine lake particles. The lake is then dried in a low-temperature oven and later milled to the customer's particular requirement.

Biology of Cochineal

Despite some controversy, cochineal apparently belongs to order Homoptera, suborder Stenorryncha, and superfamily Coccoidae, which includes all mealy bugs and scale insects (Gullan and Kosztarab 1997). The family Dactylopiidae belongs to the Neococcoidea group of the Coccoidae (Miller and Kosztarab 1979). Named by Ferris (1955), it comprises the genera *Apezcoccus, Cryptococcus, Dactylopius, Eriococcus, Gymnococcus, Kermes, Oncerotyga, Trachiococcus,* and *Xerococcus.* De Lotto (1974) has identified nine species in the genus *Dactylopius: Dactylopius autrinus* (De Lotto), *D. ceylonicus* (Green), *D. coccus* (Costa), *D. confertus* (De Lotto), *D. confusus* (Cockerell), *D. opuntieae* (Cockerell), *D. salmianus* (De Lotto), *D. tomentosus* (Lamarck), and *D. zimmermani* (De Lotto). *Dactylopius ceylonicus, D. coccus, D. confusus, D. opuntieae,* and *D. tomentosus* are abundant in the southwestern United States, Mexico, and northern South America (Miller 1976; Macgregor L. and Sampedro R. 1984).

Origin and Diversity

The center of origin and dispersal of the various species of cochineal have not been unambiguously determined. However, the place or places of origin undoubtedly are intimately related to the development and diffusion of the genera *Opuntia* and *Nopalea.* The cacti apparently originated in the neotropical regions of the Americas (southern Mexico and northern South America), and then spread both northward and southward (Gibson and Nobel 1986; Nobel 1998). Maximum diversity is found from southern Mexico to the southwestern United States. Although many platyopuntias are important for fruit and forage, *Opuntia ficus-indica* (L.) Miller is the species of greatest economic importance and is the most useful host for cochineal (Borrego and Burgos 1986). Although the range of nopal species and varieties that serve as host to the cochineal insect is ample—75, according to Portillo (1995)—those that function as natural hosts to *D. coccus* are few: notably, *O. ficus-indica* var. Castilla, *O. pilifera* Weber, *O. sarca* Griff, *O. tomentosa* Salm-Dyck, and *Nopalea cochenillifera* (L.) Salm-Dyck (Piña 1977, 1981). A number of species and varieties can, however, be artificially adapted as hosts, including several varieties of *O. amyclaea* Webber, *O. atropes* Rose, *O. jaliscana* Bravo, *O. megacantha* Salm-Dyck, and *O. streptacantha* Lemaire. In South America, *D. coccus* is reared on both spiny and spineless varieties of *O. ficus-indica* (Flores 1995; Tekelemburg 1995).

The greatest diversity of natural enemies of the nopal cactus is found in Mexico, among which are the different species of *Dactylopius.* Unfortunately, however, detailed studies of the full potential and diversity of the cochineal insect in Mexico do not exist, compared with the meticulous investigations of the parasite by Ferris (1955) and Gilreath and Smith (1988) for North America and South America and by De Lotto (1974) for South Africa. Furthermore, the wide diversity of predators and parasitoids that

TABLE 13.2
Life stage durations for *Dactylopius coccus*

Male		Female	
Stage	*Duration (days)*	*Stage*	*Duration (days)*
Emigrant nymph I	15–168	Emigrant nymph I	15–168
Cocoon construction	2–64	Nymph I	12–64
Prepupa	8–22	Nymph II	8–25
Nymph II	2–12	Mating period	2–15
Pupa	4–8	Sexual maturity	3–22
Adult	18–29	Pre-laying period	24–68
Number of females mated	0–3	Laying period	10–58
Life duration	50–89	Life duration with mating	64–150
		Life duration without mating	34–52

References: de Piña (1977); Marín and Cisneros (1977); Quispe (1983); Bustamante (1986); Vargas (1988); Velasco (1988); Cruz (1990); Méndez (1992); Montiel (1995).

prey on both wild cochineal and *D. coccus* remain to be examined.

Morphology and Life Cycle

Like other coccids, cochineal is characterized by sexual reproduction and sexual dimorphism. From the nymph I stage to the first molt, it is difficult to distinguish between the male and the female (Gunn 1978). Cytogenetically, however, males and females are quite different from the embryonic stage onward (Nur 1989; Aquino P. et al. 1994), as females have a diploid chromosome number and males are physiologically haploid. Paternal chromosomes, which look like a heterochromatic mass, are known as H chromosomes (Nur 1989). These chromosomes are inactive, but their presence is necessary for embryo viability, fertility, and sexual differentiation (Chandra 1962).

The morphology and life cycle of *D. coccus* have been extensively studied (Table 13.2). The male has a six-stage life cycle (egg, nymph I, nymph II, prepupa, pupa, adult), while the female has only four stages (egg, nymph I, nymph II, adult). Life cycle duration, morphology, and size of *D. coccus* are variable, depending on many factors, such as population density, host species, nutritional level of the host, soil quality where the host grows, light, and temperature. Despite this variability, certain characteristics are common. The egg is oval and shiny bright-red. Hatching may occur inside the adult female, or the crawlers may hatch 10 to 32 minutes after the eggs are laid. Nymph I is red and oval when recently hatched, but after a time becomes covered by a white powdery wax called coccicerin, characteristic of the species.

From 2 to 12 days after the first molt, the male as nymph II, now clearly distinct from the female, constructs a cocoon of filamentous wax. (Wild cochineal males build their cocoons on the same day as the molt.) In the prepupa stage, the antennae are relatively thick and curved backward, genitalia are distinguishable, and most meiotic activity and the greatest development of the testicles occur. In the pupa, the antennae have grown; the legs are now long and slender and lack nails. Dorsally, the segmentation of the abdomen can be seen, and ventrally the genitalia can be observed. The adult male is approximately 2.2 mm in length with a wingspan of 4.8 mm (wild cochineal males are considerably smaller). The body sections are clearly distinguishable. The antennae are moniliform (tapering), composed of 10 beadlike segments. Other features of the adult include: three pairs of simple eyes; no buccal apparatus; a pair of simple-veined, mid-thoracic wings; slender legs with a single nail; and a pair of white, waxy appendages, measuring up to 3.6 mm in length. Cruz (1990) reports that a male mates with only one to three females; reproductive efficiency is considerably reduced after more than two matings.

The nymph II female does not change form; the duration between nymph II and adult varies from 8 to 25 days (Table 13.2). The adult female is oval, 4 to 6 mm long, and 3 to 5 mm wide. Segmentation of the prosoma is barely evident (De Lotto 1974). Legs and antennae are well developed but small. The rostrum is made up of three segments (De Lotto 1974; Montiel 1995). The body has numerous (15) cuticular pores, both on the dorsum and on the abdomen, this being the characteristic commonly used by

taxonomists to classify the species (Ferris 1955; De Lotto 1974). The anal ring is recognized as a modification of segment 10; it is dorsal, has a half-moon shape, and is membranous on the anterior margin and sclerotic on the posterior margin (De Lotto 1974; Montiel 1995). Receptivity or sexual maturity occurs within 3 to 22 days. Pre-oviposition lasts from 24 to 68 days and oviposition is from 10 (when separated from the host) to 58 days. The total biological cycle of the female lasts from 64 to 150 days; during that time, a female may lay over 400 eggs.

Although it is not clear whether parthenogenetic reproduction is possible for *Dactylopius* spp., sexual reproduction is necessary for *D. coccus* and *D. confusus.* Hence, the ratio between the sexes should be 1:1 (Cruz 1990; Gilreath and Smith 1987). However, the ratio is modified by temperature (Mendez 1992) and photoperiod (Montiel 1995), generally favoring the female (Marín and Cisneros 1977). At least for *D. ceylonicus* and *D. coccus,* weather changes, especially low temperature and drought, as well as population density, affect the male population.

Host

The age of the cladodes selected and their utility for cochineal production depend on the species and variety of nopal, environmental conditions, and especially the hydration of the cladode, the quality of the soil, and the relative humidity. One-year-old, peripheral cladodes provide the most favorable conditions for cochineal establishment (Flores 1995). Five or six different kinds of nopal were utilized in Mexico for cochineal production in the 16th century. In time, most of these varieties were introduced into the West Indies and Europe. The most important nopal species for the raising of cochineal has always been *O. ficus-indica,* with its different varieties; *Nopalea cochinellifera* has also been used, but not in Mexico (Donkin 1977). Nutritional levels of nopal also affect the establishment and productivity of cochineal and its carmine content (Arteaga 1990; Vigueras and Portillo 1995). Indeed, oxalate crystals in host tissue can influence the population of cochineal (Castillo 1993).

Spines apparently have no influence on the establishment of *D. coccus.* Nevertheless, Piña (1981) indicates that, both in Mexico and in South America, cochineal occurs naturally on spiny nopal species, and under cultivation, the spiny species are more productive. Portillo (1995) reaffirms the greater adaptability of *D. coccus* to spiny varieties. Nevertheless, the nopal cacti most commonly utilized for the rearing of cochineal are spineless, for the obvious advantage of plant management. Only a weak relationship exists between the establishment of cochineal insects and stomatal frequency or the thickness of the cuticle, epidermis, and hypodermis (Castillo 1993).

Environmental Factors and Natural Enemies

Data from Mexico and other parts of the world indicate that environmental factors influence the growth and development of the cochineal insect (Piña 1977, 1981; Cruz 1990; Méndez 1992; Flores 1995; Tekelenburg 1995; Table 13.3). Important climate hazards include frosts, high temperatures (above 30°C), rainfall with its washing effects, and wind, all of which restrict the establishment of nymph colonies on the host plants. Biological hazards of the cochineal insect include predators and parasitoids, both for natural populations of wild cochineal (Gilreath and Smith 1988; Eisner et al. 1994) and for cultivated cochineal (Piña 1977). Such information can improve biological control of wild cochineal by means of its predators, as well as control of the predators by means of their parasitoids for cultivated cochineal.

Similar predators attack *D. coccus* and *D. confusus,* considerably reducing dye yields (Alzate 1831; Dahlgren 1963). The most common and dangerous predators are *Hyperaspis* sp. (Coccinelidae, Coleoptera), *Chilocorus* spp. (Coccinelidae), "drum worm" (*Bacca* sp., Syrphidae: Diptera), *Laetilia* sp. (Pyralidae: Lepidoptera), *Sympherobius* sp. (Neuroptera), and *Sapingogaster texana* (Syrphidae; Piña 1977; Gilreath and Smith 1988). *Homalotylus cockerella* is a parasitoid of *Hyperaspis trifurcata* (Gilreath and Smith 1988). In Mexico, several parasitoids of the family Pteromalidae have been identified for *Sapingogaster texana* (Syrphidae)—*Brachimeria conica, Spilochalcis flavopicta* (Chalcididae), and *Temelucha* sp. (Ichneumonidae; Gilreath and Smith 1988)—and mites belonging to the family Piemotidae have been identified as parasitoids for *Laetilia* sp. In greenhouse rearings, some parasitoids (Pteromalidae) attack both cochineal and its predators (*Hyperaspis* sp.).

D. coccus *versus Wild Cochineal*

Two characteristics distinguish *D. coccus* from wild cottony cochineal. First, the wild insects produce a waxy, cottonlike coating, which is abundant, loose, soft, and thermally stable on the dorsal side, but compact and resistant on the ventral side, permitting firm adherence of the insect to the host platyopuntia; this coating makes the parasite resistant to wind and rain. Second, wild cochineal yields a much lower concentration of carmine colorant, from 2 to 7% by dry weight, whereas yields from *D. coccus* are 15 to 25%. Among other characteristics of the wild species is the ability to transmit disease to the host (Miller 1976), which in

TABLE 13.3
Environmental parameters influencing *D. coccus*

Factor	Range	Optimal	Observations
Mean temperature (°C)	20–32	26–28	Cochineal can tolerate temperature extremes below 0°C or above 36 to 40°C; the effects depend on the duration of exposure.
Light (% of maximal)	40–60	50	Can be controlled by shading; the amount of light required interacts with the temperature.
Relative humidity (%)	30–60	40	Estimated, as parameters are not fully studied.
Annual rainfall (mm)	0–600	0–100	Depending on the temperature, cochineal can be raised in areas of greater or lesser rainfall, but with protection and, if necessary, irrigation.
Altitude (m)	0–2,300	200–1,800	Not a limiting factor, if temperature and radiation are in the appropriate ranges.
Soil type	Alluvium	Volcanic	Limestone soils, or soils with high calcium or magnesium contents, are apparently not favorable.

addition to its short biological cycle, high reproductive potential, and high resistance to climatic factors, makes wild cochineal very useful in the control of weedy nopal (Zimmermann and Moran 1991; Chapter 14). However, it is also a dangerous competitor of *D. coccus. Dactylopius coccus,* on the other hand, is distinguished by its fine, waxy coating, which takes the form of a powder. Apart from its buccal apparatus, *D. coccus* has no other structure that aids its adherence to the surface of a cladode, making it more susceptible to environmental hazards.

Cytogenetically, all analyzed wild cochineal species have a chromosome number of $n = 5$ and similar chromosomal karyotypes: a long chromosome three times the average length and four short chromosomes (Aquino P. et al. 1994). *Dactylopius coccus* has a chromosome number of $n = 8$ and a different karyotype—all the chromosomes are short. The four longest chromosomes of *D. coccus* do not differ from those of their possible homologue in wild cochineal, and the length of the long wild cochineal chromosome equals the length of the sum of the four shortest chromosomes of *D. coccus* (Aquino P. et al. 1994). Thus, cochineal insects apparently eliminate meiosis II by a simple chromosomal segregation. *Dactylopius coccus* has a very low frequency of "normal" meiosis II, whereas wild species, such as *D. confusus,* have a high frequency of "normal" meiosis II (Aquino P. et al. 1994).

Coccidae generally have evolved toward an increase in chromosome number by means of chromosome fragmentation (Nur et al. 1987; Nur 1989). This has apparently occurred for both *D. coccus* and wild cottony cochineal. Nevertheless, a chromosome breakup usually produces more disadvantages than advantages, and three fragmentations (which is what presumably occurred for *D. coccus*) could make the survival of the progeny more difficult. However, two additional modifications in the chromosomes of this insect group would increase the possibilities of survival of mutant individuals: (1) the presence of a diffuse centromere and (2) the inversion of the meiotic sequence (Chandra 1962). This permits balanced meiosis and equal separation of the chromosome groups, thereby reducing the loss of chromosome fragments—an irreconcilable loss in species with a defined centromere.

Marketing of Cochineal

Production and Prices

Since pre-Hispanic times in America, the cochineal market has been heavily affected by political and natural events, which have had much influence on production and prices. The highest prices for cochineal have always coincided with periods of prosperity in the principal consumer countries—historically England, France, Germany, and Holland, and at present, Italy, Japan, and the United States (Alzate 1831; Houghton 1877; Dahlgren 1963; Brana 1964; Donkin 1977; EPTASA 1983; Avila and Remond 1986; Contreras S. 1996; P. Quintanilla, personal communication; J. A. Bustamante, personal communication). The most favorable prices for cochineal possibly occurred from 1765 to 1775, when 520 metric tons (1 ton = 1,000 kg) were produced annually; the period from 1799 to 1833 was also a time of bonanza, although annual worldwide production had dropped to 190 tons, again almost all from Mexico. After this period, production and prices began to drop in Mexico in response to fierce competition from 1825 to 1880

from Guatemala and the Canary Islands. The Guatemalan market flourished from 1830 to 1865, but was overtaken by the booming Canary Islands' production from 1849 to 1882, despite the fact that world prices for cochineal had been in gradual decline since 1831. The main advantage for the Canary Islands was probably geographic—proximity to the main European consumer countries. Soaring production and lower shipping prices of Canary Islands' cochineal were probably the reasons for the drop in demand for the Guatemalan and Mexican dye; South American cochineal, meanwhile, had been in a slump since the turn of the 17th century. The Canary Islands' production continued from 1880 to 1927, albeit at lower levels and lower prices, due to the introduction of synthetic dyes; annual production averaged approximately 80 tons for 1927 to 1929 and currently is 40 tons year^{-1}.

Although little information is available for South American cochineal production for 1750 to 1935, production was apparently over 1,000 tons for 1829 to 1859 (Brana 1964; Donkin 1977). Records of the Peruvian market appear in 1937 and show a linear increase since that date, becoming 100 tons by 1975 (Fig. 13.8A). From 1975 to 1990, Peru cornered the world market, with a share of up to 95%. Since 1990, Argentina, Bolivia, and Chile have entered the world market, causing a reduction in Peru's domination. Indeed, Peru's bulk exportation of the raw material since 1997 has diminished, and a greater volume is being consigned to processed dye (Fig. 13.8).

Supply and Demand

Presently Peru is the world's most important producer of cochineal. In response to increasing demand, Peru's production increased sixfold from 1975 to 1998, reaching 650 tons (Fig. 13.8A). Since 1983, Peru has steadily increased its industrial processing capacity for cochineal; since 1986 most of the exported cochineal has been processed (Fig. 13.8A). The price of cochineal has fluctuated widely, generally being below U.S. $20 per kilogram but reaching $40 in 1985 and $75 in 1996 (Fig. 13.8B). Prices of refined carminic acid, which accounts for about 10% of the dye export, tripled from 1994 to 1996, when it reached $400 per kg then decreased twofold by 1998, indicating the volatility of the market. If competition from synthetic dye manufacturers can be surmounted and if cochineal dye is internationally certified, the demand should increase.

Chile entered the world market in 1997 with a production of approximately 150 tons. Traditionally, Spain had 5 to 10% of world production, or approximately 65 tons. Peru, Chile, and Spain recently have annually supplied the world marketplace with 755 tons of cochineal. Moreover,

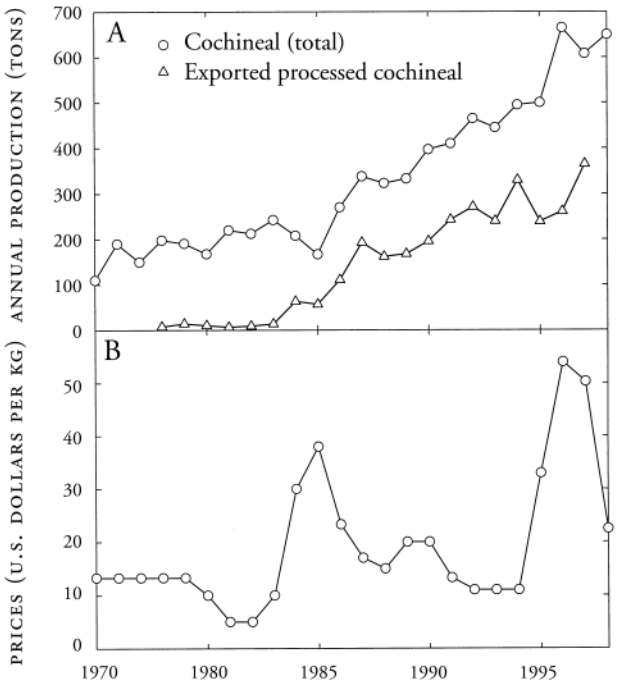


Figure 13.8. Peruvian cochineal production and prices for 1975 to 1998: (A) total production (○) and exportation of processed cochineal (Δ), and (B) prices for processed cochineal. References: Avial and Redmond (1986); EPTASA (1983); Contreras S. (1996); P. Quintanilla (personal communication); J. A. Bustamante (personal communication).

Chile and Peru have predicted increases in production, meaning that the annual supply of the dye from these three countries should approach 1,000 tons.

Conclusions and Future Prospects

A common way to consume cladodes in Mexico is as nopalitos. After despining, minimal processing facilitates consumption of the tender young pads. Nopalitos can be further processed in brine or pickled. The consumption of the young pads not only should increase the cultivation of *Opuntia ficus-indica* and consequently the use of arid lands in many regions of the world, but also should serve as a healthful food due mainly to the dietary fiber content. Dietary fiber increases with stem age, opening up other ways to process and use this part of platyopuntias in addition to the currently more popular use of young pads. Such use could be introduced into those countries where *O. ficus-indica* is presently only a fruit crop. The different alternatives for processing and consuming nopal and nopalitos require educating the consumers, including full information on the nutritional value of the cladodes and technology transfer. The processes used today are quite simple and do not require expensive equipment. The food

industry can utilize similar processes already installed for other raw vegetables. The properties of cladodes to alleviate illnesses, such as diabetes and obesity, should be studied more to confirm their effectiveness. Mucilage has great potential as a thickener in foods and an adhesive in paints, but again these properties must be studied in greater detail.

The dye insect *Dactylopius coccus* has enjoyed great importance worldwide since its discovery in Mexico in the 16th century. Cochineal is valued not only as the source of a red colorant, useful in a number of products for human consumption, but also as a biological control of weedy nopal infestations in some parts of the world. Its importance as a colorant has made it the subject of scientific, economic, and historical inquiry since the late 18th century. The most advanced investigations undertaken so far have been historical, chemical, and toxicological, whereas the biology of the parasitic insect has been largely ignored until recently. Genetic and biosynthetic aspects, as well as the host (*Opuntia* spp.)–parasite (*Dactylopius* spp.) interaction, have not received enough attention (Joshi and Lambdin 1996). For these reasons, it is presently difficult to determine the phylogenetic and evolutionary relationships, as well as the agronomic techniques, that would maximize the potential of both susceptible host cacti and *D. coccus.*

Acknowledgments

The authors thank anthropologist Jodie Randall for her comments regarding cochineal history and Mayra Perez Sandi y Cuen (Mac Arthur Foundation) for providing information on the cochineal trade.

Literature Cited

Albornoz, N. 1998. *Elaboración y Evaluación de una Crema de Verduras con Adición de Fibra Dietética de Nopal.* Facultad de Ciencias Agrarias y Forestales. Universidad de Chile, Santiago.

Ali, M. A., and L. J. Haynes. 1959. C-Glycosyl compounds. Part III. Carminic acid. *Journal of the Chemical Society:* 1033–1035.

Alzate, J. A. 1831. *Memoria acerca del insecto grana o cochinilla, su naturaleza y serie de su vida, método de propagarlo y reducirlo al estado en que forma uno de los ramos más útiles del comercio* (Written in 1777). Imprenta del Aguila, Mexico City.

Amin, El-S., O. M. Awad, and M. M. El-Sayed. 1970. The mucilage of *Opuntia ficus-indica. Carbohydrate Research* 15: 159–161.

Aquino, P., G., A. García V., T. Corona T., and N. M. Bárcenas O. 1994. Estudio cromosómico de cuatro especies de cochinilla del nopal (*Dactylopius* spp.) (Homoptera: Dactylopiidae). *Agrociencia, serie Fitociencia* 5: 7–23.

Arteaga, J. L. 1990. Influencia de la fertilización N-P-K en la producción de cochinilla (*Dactylopius coccus* Costa). Bachelor's Thesis, Universidad Nacional de San Cristóbal de Huamanga, Ayacucho, Peru.

Avena, B. R. S. 1996. Proceso de hortalizas pre-cortadas. *Boletín del Centro de Investigación en Alimentos y Desarrollo, A.C.* 5: 7–8.

Avila, R., and Z. Remond. 1986. *Estudio Técnico de la Cochinilla.* Dirección de Servicios Técnicos, División de Extracción Industrial (ITINTEC), Lima, Peru.

Badillo, J. R. 1987. Elaboración de una jalea de nopal. Bachelor's Thesis, Escuela de Ciencias Químicas, Universidad Autónoma de Puebla, Puebla, Mexico.

Barbera, G. 1991. Utilizzazione economica delle Opunzie in Messico. *Frutticoltura* 2: 41–48.

Borrego, F., and N. Burgos. 1986. *El Nopal.* Universidad Autónoma Agraria Antonio Narro, Saltillo, Mexico.

Brana, D. D. 1964. Cochineal: Aboriginal dyestuff from Nueva España. In *Actas y Memorias del XXXVI Congreso Internacional de Americanistas.* University of Texas, Austin. Pp. 77–91.

Brecht, J. K. 1995. Physiology of lightly processed fruits and vegetables. *HortScience* 30: 18–24.

Bustamante, O. 1986. Estudio del ciclo biológico de la cochinilla (*Dactylopius coccus* Costa) en su ambiente natural en Ayacucho. In *Resúmenes del 1er. Congreso Nacional de Tuna y Cochinilla.* Ayacucho, Peru. Pp. 44–45.

Cantwell, M. 1991. Quality and postharvest physiology of "nopalitos" and "tunas." *Proceedings of the 2nd Annual Texas Prickly Pear Conference.* McAllen, Texas. Pp. 50–66.

Cantwell, M. 1992. Postharvest handling systems: Minimally processed fruits and vegetables. In *Postharvest Technology of Horticultural Crops* (A. A. Kader, ed.). Division of Agriculture and Natural Resources, Publication 3311. University of California, Davis. Pp. 227–281.

Cantwell, M. 1995. Post-harvest management of fruits and vegetable stems. In *Agro-ecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 120–136.

Cantwell, M., A. Rodríguez-Felix, and F. Robles-Contreras. 1992. Postharvest physiology of prickly pear cactus stems. *Scientia Horticulturae* 50: 1–9.

Cárdenas, A., and F. Goicoolea 1997. Reología en solución del mucílago del nopal (*Opuntia ficus-indica*). In *Memorias VII Congreso Nacional y V Internacional Conocimiento y Aprovechamiento del Nopal.* Monterrey, Mexico. Pp. 171–172.

Cárdenas, A., I. Higuera-Ciapara, and F. M. Goicoolea. 1997. Rheology and aggregation of Cactus (*Opuntia ficus-indica*) mucilage in solution. *Journal of the Professional Association for Cactus Development* 2: 152–159.

Castillo V., J. 1993. Relación entre algunas características anatómicas y químicas del nopal (*Opuntia* sp.) y el establecimiento de la cochinilla (*Dactylopius coccus* Costa). Bachelor's Thesis, Departamento de Fitotécnia, Universidad Autónoma Chapingo, Chapingo, Mexico.

Chandra, H. S. 1962. Inverse meiosis in triploid female of the mealy bugs, *Planococcus citri. Genetics* 47: 1441–1454.

Chang, L. A., L. K. Hammet, and D. M. Pharr. 1982. Ethanol, alcohol dehydrogenase and pyruvate decarboxylase in storage roots of four sweet potato cultivars during simulated flood damage and storage. *Journal of the American Society for Horticultural Science* 107: 674–677.

Colin, B.C. 1976. Industrialización del nopal y sus productos. *Tecnología Laboratorios Nacionales de Fomento Industrial* II: 11–13.

Contreras S., A. C. 1996. *Capital Comercial y Colorantes en la Nueva España: Segunda mitad del siglo XVIII.* El Colegio de Michoacán y Universidad Autónoma de Yucatán, Mérida, Mexico.

Corrales, G. J. 1992a. Descripción y análisis de la cosecha y del manejo en fresco de nopalito y tuna. In *Memoria de Resúmenes del 5to. Congreso Nacional y 3er. Congreso Internacional Conocimiento y Aprovechamiento del Nopal.* Universidad Autónoma de Chapingo, Mexico. P. 109.

Corrales, G. J. 1992b. Perspectivas de industrialización de nopalito y tuna. In *Memoria de Resúmenes del 5to. Congreso Nacional y 3er. Congreso Internacional Conocimiento y Aprovechamiento del Nopal.* Universidad Autónoma de Chapingo, Chapingo, Mexico. Pp. 97–98.

Corrales-García, J. 1997. Postcosecha de la tuna y del nopal verdura. In *Memorias del VII Congreso Nacional y V Internacional Conocimiento y Aprovechamiento del Nopal.* Facultad de Agronomía, Universidad Autónoma de Nuevo León, Monterrey, México. Pp. 88–98.

Corrales-García, J. 1998. Industrialization of prickly pear pads (nopalitos). In *Proceedings of the International Symposium Cactus Pear and Nopalitos Processing and Uses.* Universidad de Chile, Santiago. Pp. 25–32.

Cruz, M. 1990. Determinación de algunos aspectos biológicos de la grana-cochinilla del nopal (*Dactylopius coccus* Costa) (Coccoidea: Dactylopiidae) en Chapingo, México. Bachelor's Thesis, Universidad Autónoma de Chapingo, Chapingo, Mexico.

Dahlgren, B. 1963. *La Grana o Cochinilla.* Nueva Biblioteca Mexicana de Obras Históricas Vol. I, Editorial José Porrúa Hermanos, Mexico City.

De Lotto, G. 1974. On the status of an identity of the cochineal insect (Homoptera: Coccoidea: Dactylopiidae). *Journal of the Entomological Society of South Africa* 37: 167–193.

De Sahagún, B. 1829. Historia general de las cosas de Nueva España. In *Sepan Cuantos* (A. M. Garibay E., ed.). Editorial Porrua, Mexico City.

Donkin, R. A. 1977. Spanish red: An ethnogeographical study of cochineal and the *Opuntia* cactus. *Transactions of the American Philosophical Society* 67: 63–77.

Eisner, T., R. Ziegler, J. L. McCormick, M. Eisner, E. R. Hoebeket, and J. Meinwald. 1994. Defensive use of an acquired substance (carminic acid) by predaceous insect larvae. *Experientia* 50: 610–615.

EPTASA (Estudios de Planificación y Técnica Aplicada, S. A.). 1983. *Estudio sobre la producción y comercialización de cochinilla y carmín de cochinilla.* Ministerio de Agricultura Pesca y Alimentación, Madrid, Spain.

Fernández, M. L., A. Trejo, and D. McNamara. 1990. Pectin isolated from prickly pear (*Opuntia* sp.) modifies low density lipoprotein metabolism in cholesterol-fed guinea pigs. *Journal of Nutrition* 120: 1283–1290.

Ferris, G. F. 1955. Family Dactylopiidae Fernald. In *Atlas of the Scale Insects of North America.* Stanford University Press, Stanford, California. Pp. 69–217.

Fiecchi, A., M. Anastasia, G. Galli, and P. Gariboldi. 1981. Assignment of the β configuration to the C-glycosyl bond in carminic acid. *Journal of Organic Chemistry* 46: 1511.

Flores, V. 1995. Crianza de la cochinilla en Sudamérica. In *Memorias del 6to. Congreso Nacional y 4to. Congreso Internacional sobre el Conocimiento y Aprovechamiento del Nopal.* Universidad de Guadalajara, Zapopan, Mexico. Pp. 35–47.

Flores, V. C. 1997. La producción de nopalito en México. In *Memorias del VII Congreso Nacional y V Inter-*

nacional Conocimiento y Aprovechamiento del Nopal. Monterrey, Mexico. Pp. 28–38.

Fontanot, M. 1999. Elaboración de galletas de avena con adición de harina de nopal rica en fibra dietética. Master's Thesis, Universidad de Chile, Santiago.

Ford, G. P., T. Gopal, D. Grant, I. F. Gaunt, J. G. Evans, and W. H. Butler. 1987. Chronic toxicity/carcinogenicity study of carmine of cochineal in the rat. *Food and Chemical Toxicity* 25: 897–902.

Frati-Munari, A. C., L. M. Del Valle-Martínez, C. R. Araiza-Andraca, S. Islas-Andrade, and A. Chávez-Negrete. 1989. Hypoglycemic effect of different doses of nopal (O*puntia streptacantha*) in patients with type II diabetes mellitus. *Archivos de Investigación Medica* 20: 197–201.

Frati-Munari, A., E. Jiménez, and C. R. Ariza. 1990. Hypoglycemic effect of *Opuntia ficus-indica* in non insulin-dependent diabetes mellitus patients. *Phytotherapy Research* 40: 195–197.

Frati-Munari, A., O. Vera Lastras, and C. R. Ariza Andraca. 1992. Evaluación de cápsulas de nopal en diabetes mellitus. *Gaceta Médica de México* 128: 431–436.

Gallardo, Y., M. L. Zambrano, and A. D. Hernandez. 1997. Determinación de las propiedades fisicoquímicas del nopal verdura. In *Memorias VII Congreso Nacional y V Internacional Conocimiento y Aprovechamiento del Nopal.* Monterrey, Mexico. Pp. 277–278.

García, J. R. 1993. Análisis de Factibilidad Técnico, económico y financiero de una planta procesadora de nopal en escabeche. Bachelor's Thesis, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico City.

Gardiner, D., P. Felker, and T. Carr. 1999. Cactus extract increases water infiltration rates in two soils. *Communications in Soil Science and Plant Analysis* 30: 1707–1712.

Gibson, A. C., and P. S. Nobel 1986. *The Cactus Primer.* Harvard University Press, Cambridge, Massachusetts.

Gilreath, E. M., and J. W. Smith Jr. 1987. Bionomics of *Dactylopius confusus* (Homoptera: Dactylopiidae). *Annals of Entomological Society of America* 80: 768–774.

Gilreath, E. M., and J. W. Smith. 1988. Natural enemies of *Dactylopius confusus* (Homoptera: Dactylopiidae) exclusion and subsequent impact on Opuntia (Cactaceae). *Environmental Entomology* 17: 730–738.

Goldstein, G., and P. S. Nobel. 1991. Changes in osmotic pressure and mucilage during low-temperature acclimation of *Opuntia ficus-indica. Plant Physiology* 97: 954–961.

Granados, D., and A. D. Castañeda. 1991. *El Nopal. Historia, Fisiología, Genética e Importancia Frutícola.* Editorial Trillas, Mexico City.

Grant, D., I. F. Gaunt, and F. M. B. Carpanini. 1987. Teratogenicity and embriotoxicity study of carmine of cochineal in the rat. *Food and Chemical Toxicity* 25: 913–917.

Grant, D., and I. F. Gaunt. 1987. Three generation reproduction study on carmine of cochineal in rat. *Food and Chemical Toxicity* 25: 903–912.

Grijspaardt-Vink, C. 1996. Ingredients for healthy foods featured at European expo. *Food Technology* 2: 30.

Gulías, A., and G. Robles. 1989. El nopal en su justa medida. *Cuadernos de Nutrición* 12: 42–43.

Gullan, P. J., and M. Koszarab. 1997. Adaptations in scale insects. *Annual Review of Entomology* 42: 23–50.

Gunn, B. H. 1978. Sexual dimorphism in the first instar of the cochineal insect *Dactylopius austrinus* De Lotto (Homoptera: Dactylopiidae). *Journal of the Entomological Society of South Africa* 41: 333–338.

Hegwood, D. 1990. Human health discoveries with *Opuntia* sp. (Prickly pear). *HortScience* 25: 1515–1516.

Hernández, A. D., G. Chamorro, and Y. Gallardo. 1997. Efecto fisiológico de la ingesta de nopal sobre la producción de heces fecales. In *Memorias VII Congreso Nacional y V Internacional Conocimiento y Aprovechamiento del Nopal.* Monterrey, Mexico. Pp. 289–290.

Hernández, A. D., Y. Gallardo, and G. Chamorro. 1998. Caracterización de la fibra de nopal por medio de su respuesta fisiológica. In *Fibra Dietética* (F. Lajolo and E. Wenzel, eds.). Temas en Tecnología de Alimentos, Vol. 2. Instituto Politécnico Nacional, Mexico City. Pp. 215–230.

Hollingsworth, P. 1996. Food trends: Diversity and choice dominate. *Food Technology* 5: 40.

Houghton, H. 1877. *La Cochinilla: Memoria Demostrativa de las Causas que han Producido la Decadencia de este Renglón de Comercio en los Ultimos Años.* Sociedad Económica de Amigos del País, Gran Canaria, Spain.

Ibañez-Camacho, R., and R. Roman Ramos. 1979. Efecto hipoglucemiante del nopal. *Archivos de Investigación Médica* 10: 223–230.

Ibañez-Camacho, R., M. Meckes-Lozoya, and V. Mellado-Campos. 1983. The hypoglycemic effect of *Opuntia*

streptacantha studied in different animal experimental models. *Journal of Ethnopharmacology* 7: 175–181.

ITINTEC (Instituto Nacional de Investigación Tecnológica Industrial y de Normas Técnicas, Perú). 1990. Perfil Industrial: Producción de carmin a partir de la cochinilla. *Información Tecnológica* 16: 33–36.

Joshi, P. A., and P. L. Lambdin. 1996. The ultrastructure of hemocytes in *Dactylopius confusus* (Cockerell), and the role of granulocytes in the synthesis of cochineal dye. *Protoplasma* 192: 199–216.

Kader, A. A. 1986. Biochemical and physiological basis for effects of controlled and modified atmospheres on fruits and vegetables. *Food Technology* 40: 99–104.

Kawasaki, Y., T. Umemura, K. Sai, R. Hasegawa, J. Momma, M. Saitoh, Y. Matsushima, Y. Nakaji, M. Tsuda, and Y. Kurokawa. 1994. A 13-week toxicity study of simultaneous administration of cochineal and aluminum potassium sulfate in rats. *Bulletin of the National Institute of Health Sciences* 112: 48–56.

Lecaros, M. 1997. *Caracterización de Harina de Cladodio de Nopal* (*Opuntia ficus-indica*). Universidad de Chile, Santiago.

Loik, M. E., and P. S. Nobel. 1991. Water relations and mucopolysaccharide increases for a winter hardy cactus during acclimation to subzero temperatures. *Oecologia* 86: 340–346.

Macgregor L., R., and G. Sampedro R. 1984. Catálogo de cóccidos mexicanos familia Dactylopiidae (Homoptera-Coccidae). *Anales del Instituto de Biología (Serie Zoología), Universidad Nacional Autónoma de México* 54: 217–223.

Marín L., R., and V. Cisneros F. 1977. Biología y morfología de la cochinilla del carmín (*Dactylopius coccus* Costa) Homoptera: Dactylopiidae. *Revista Peruana de Entomología* 29: 115–120.

McGarvie, D., and P. H. Parolis. 1979a. The mucilage of *Opuntia ficus-indica. Carbohydrate Research* 69: 171–179.

McGarvie, D., and P. H. Parolis. 1979b. The mucilage of *Opuntia ficus-indica.* Part 2. The degraded polysaccharide. *Journal of the Chemical Society, Perkin Transactions* 1: 1464–1466.

McGarvie, D., and P. H. Parolis. 1981. Methylation analysis of the mucilage of *Opuntia ficus-indica. Carbohydrate Research* 88: 305–314.

Meckes, L. M., and R. Roman-Ramos. 1986. *Opuntia streptacantha:* A coadjutor in the treatment of diabetes mellitus. *American Journal of Chinese Medicine* 14: 116–118.

Méndez, G., S. J. 1992. Tasas de supervivencia y reproducción de la grana-cochinilla *Dactylopius coccus* Costa (Homoptera:Dactylopiidae) a diferentes temperaturas. Master's Thesis, Colegio de Postgraduados, Chapingo, Mexico.

Miller, D. H. 1976. Dactylopiidae. In *Syllabus for workshop on scale insect identification. Proceedings of National Meeting of the Entomological Society of America* (J. W. Beradsley and U. Nur, eds.), Honolulu. Pp. 1–10.

Miller, D. R., and M. Kosztarab 1979. Recent advances in the study of scale insect. *Annual Review of Entomology* 24: 1–27.

Montiel R., M. L. 1995. Morfología de *Dactylopius coccus* Costa (Homoptera: Dactylopiidae) y su biología y producción en dos fotoperiodos. Master's Thesis, Colegio de Postgraduados, Montecillo, Mexico.

Mulas, M. 1993. Medicinal properties and yield possibilities of the prickly pear (*Opuntia* spp.) in the mediterranean environment. *Acta Horticulturae* 331: 79–84.

Nerd, A., M. Dumotier, and Y. Mizrahi. 1997. Properties and postharvest behaviour of the vegetable cactus *Nopalea cochenillifera. Postharvest Biology and Technology* 10: 135–143.

Nobel, P. S. 1998. *Los Incomparables Agaves y Cactos.* Editorial Trillas, Mexico City.

Nobel, P. S, J. Cavelier, and J. L. Andrade. 1992. Mucilage in cacti: Its apoplastic capacitance, associated solutes, and influence on tissue water relations. *Journal of Experimental Botany* 43: 641–648.

Nur, U. 1989. Chromosomes, sex-ratios and sex determination: Reproductive biology and genetics. In *Armored Scale Insects, Their Biology, Natural Enemies and Control. Vol. A.* (D. Rosen, ed.). Elsevier Science Publishers, Amsterdam. Pp.179–190.

Nur, U., S. W. Brown, and J. W. Beardsley. 1987. Evolution of chromosome number in mealy bugs (Pseudoccidae: Homoptera). *Genetica* 71: 53–60.

Paulsen, B. S., and P. S. Lund. 1979. Water-soluble polysaccharides of *Opuntia ficus-indica* cv. "Burbank's spineless." *Phytochemestry* 18: 569–571.

Perez, J. A. 1992. Anteproyecto de una planta procesadora de grana cochinilla para la obtención de sus principales derivados: extracto de cochinilla, carmin de cochinilla y acido carmínico. Bachelor's Thesis, Universidad La Salle, Mexico City.

Periago, M. J., G. Ros, G. López, M. C. Martinez, and F. Rincón. 1993. The dietary fiber components and their physiological effects. *Revista Española de Ciencia y Tecnología de Alimentos* 33: 229–246.

Pimienta Barrios, E. 1990. *El Nopal Tunero.* Universidad de Guadalajara, Zapopan, Mexico.

Piña L., I. 1977. *La Grana o Cochinilla del Nopal.* Laboratorios Nacionales de Fomento Industrial de México, Mexico City.

Piña, L., I. 1981. Observaciones sobre la grana y sus nopales hospederos en el Perú. *Cactáceas y Suculentas de México* 26: 10–15.

Portillo, M. L. 1995. Los hospederos de las cochinillas del carmín (*Dactylopius* spp.) y algunas consideraciones sobre su aprovechamiento. In *Memorias del 6to Congreso Nacional y 4to Congreso Internacional Conocimiento y Aprovechamiento del Nopal.* Universidad de Guadalajara, Zapopan, Mexico. Pp. 35–47.

Quirce, S., M. Cuevas, J. M. Olaguibel, and A. I. Tabar. 1994. Occupational asthma and inmmulogical responses induced by inhaled carmine among employees at a factory making natural dyes. *Journal of Allergy and Clinical Immunology* 93: 44–52.

Quispe, I. 1983. Ciclo biológico de la cochinilla del cactus *Dactylopius coccus* Costa. En diferentes épocas del año y en tres pisos altitudinales en Ayacucho. In *Memorias del primer seminario Departamental de Producción y Fomento de Tuna y Cochinilla.* Ayacucho, Peru. Pp. 44–45.

Ramayo-Ramírez, L., C. Saucedo-Veloz, and S. Lakshminarayana. 1978a. Causas de altas pérdidas en nopal hortaliza (*Opuntia inermis* Coulter) almacenado por refrigeración y su control. *Chapingo Nueva Época* 10: 33–36.

Ramayo-Ramírez, L., C. Saucedo-Veloz, and S. Lakshminarayana. 1978b. Prolongación de la vida de almacenamiento del nopal hortaliza (*Opuntia inermis* Coulter) por refrigeración. *Chapingo Nueva Época* 10: 30–32.

Ramírez, G., and C. Aguilar. 1995. The effect of Opuntia in lowering serum glucose among NIDDM patients. A systematic review—preliminary findings. In *Proceedings: I Conference of the Professional Association for Cactus Development.* Kingsville, Texas. Pp. 71–78.

Rodríguez, D. 1999. Desarrollo de una bebida pasteurizada a base de nopal. In *Memorias. VIII Congreso Nacional y VI Internacional Conocimiento y Aprovechamiento del Nopal.* San Luis Potosí, Mexico. Pp. 75–76.

Rodríguez-Félix, A., and H. Soto-Valdez. 1992. Quality changes of diced nopal during storage in polyethylene bags. In *Proceedings of the 3rd Annual Texas Prickly Pear Conference, Texas Prickly Pear Council.* McAllen, Texas. Pp. 22–25.

Rodríguez-Felix, A., and M. A. Villegas-Ochoa. 1998. Postharvest handling of cactus leaves (nopalitos). In *Proceedings of the International Symposium "Cactus Pear and Nopalitos Processing and Uses."* Universidad de Chile, Santiago. Pp. 7–16.

Rosado, J., and M. Díaz. 1995. Propiedades fisicoquímicas relacionadas con función gastrointestinal de seis fuentes de fibra dietética. *Revista de Investigación Clinica* 47: 283–289.

Ross, G. N. 1986. The bug in the rug. *Natural History* 86: 67–71.

Sáenz, C. 1995. Food manufacture and by-products. In *Agro-ecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 137–143.

Sáenz, C. 1998. Cladodes: A source of dietary fiber. *Journal of the Professional Association for Cactus Development* 2: 117–123.

Sáenz, C., M. Vásquez., S. Trumper, and C. Fluxá. 1992. Extracción y composición química de mucílago de tuna (*Opuntia ficus indica*). In *Actas: II Congreso Internacional de la Tuna y Cochinilla.* Santiago, Chile. Pp. 93–96.

Sáenz, C., E. Sepúlveda, and M. Moreno. 1995a. Estudio de formulaciones para la obtención de mermelada de nopal (*Opuntia ficus-indica*). In *Resúmenes: XI Congreso Nacional de Ciencia y Tecnología de Alimentos.* Viña del Mar, Chile. P. 163.

Sáenz, C., E. Sepúlveda, M. Moreno, D. Granger, and N. Pak. 1995b. Características funcionales de harina de nopal (*Opuntia ficus-indica*) y su utilización en la formulación de galletas. In *Actas: VI Congreso Nacional y IV Congreso Internacional Conocimiento y Aprovechamiento del Nopal,* Guadalajara, Mexico. Pp. 24–27.

Sáenz, C., N. Pak, E. Sepúlveda, and M. Lecaros. 1997. Caracterización de harina de cladodio de nopal. In *Memorias: VII Congreso Nacional y V Internacional sobre Conocimiento y Aprovechamiento del Nopal.* Monterrey, Mexico. Pp. 302–303.

Saltveit, M. E., Jr., and L. L. Morris. 1990. Overview on chilling injury of horticultural crops. In *Chilling Injury of Horticultural Crops* (C. Y. Wang, ed.). CRC Press, Boca Raton, Florida. Pp. 3–15.

Saltzman, M. 1992. Identifying dyes in textiles. *American Scientist* 80: 474–481.

Schlimme, D.V. Marketing lightly processed fruits and vegetables. *HortScience* 30: 15–17.

Sepúlveda, E., C. Sáenz, and M. Moreno. 1995. Obtención y caracterización de harina de nopal (*Opuntia ficus-indica*). In *Actas: VI Congreso Nacional y IV Congreso Internacional sobre Conocimiento y Aprovechamiento del Nopal.* Guadalajara, Mexico. Pp. 28–31.

Sloan, E. 1994. Top ten trends to watch and work on. *Food Technology* 7: 89–100.

Spiller, G. 1992. Definition of dietary fiber. In *Dietary Fiber in Human Nutrition,* 2nd ed. (G. A. Spiller, ed.). CRC Press, Boca Raton, Florida. Pp. 15–18.

Sugimoto, N., Y. Goda, J. Suzuki, M. Kuroyanagi, T. Yamada, K. Yoshihira, and T. Maitani. 1998. Structure of minor pigments in cochineal dye. *Natural Medicines* 52: 135–139.

Tekelemburg, A. 1995. La producción de cochinilla (*Dactylopius coccus* Costa) en ambientes semicontrolados. In *Memorias VI Congreso Nacional y IV Congreso Internacional Conocimiento y Aprovechamiento del Nopal.* Universidad de Guadalajara, Zapopan, Mexico. Pp. 48–55.

Tirado, L. E. 1986. Elaboración de una mermelada a base de nopal. Bachelor's Thesis, Universidad Autónoma de Puebla, Puebla, Mexico.

Trachtenberg, S., and A. M. Mayer. 1981. Composition and properties of *Opuntia ficus-indica* mucilage. *Phytochemistry* 20: 2665–2668.

Trejo, A., G. G. Ortiz., A. M. Puebla, M. D. Huizar, M. R. Munguía, S. Mejía, and E. Calva. 1995. A purified extract from prickly pear cactus (*Opuntia* sp.) controls experimentally induced diabetes in rats. In *Actas: VI Congreso Nacional y IV Congreso Internacional sobre Conocimiento y Aprovechamiento del Nopal.* Guadalajara, Mexico. Pp. 300–305.

Trejo-Gonzalez, A., E. Calva, P. J. Monterrubio, R. Hernández, L. Sánchez, J. Terrazas, M. A. Ruida, and B. Cobos. 1991. Antidiabetic properties of prickly pear cactus. In *Proceedings of the 2nd Annual Texas Prickly Pear Council.* Kingsville, Texas. Pp. 75–78.

Trejo, A., G. G. Ortiz., A. M. Puebla, M. D. Huizar, M. R. Munguía, S. Mejía, and E. Calva. 1995. A purified extract from prickly pear cactus (*Opuntia* sp.) controls experimentally induced diabetes in rats. In *Actas: VI Congreso Nacional y IV Congreso Internacional sobre Conocimiento y Aprovechamiento del Nopal.* Guadalajara, Mexico. Pp. 300–305.

Tütem, E., R. Apak, and K. Sözguen. 1996. The interaction of antitumor-active anthraquinones with biologically important redox couples: I. Spectrophotometric investigation of the interaction of the carminic acid and mitoxantrone with the Iron (II, III) and copper (I, II) redox couples. *Journal of Inorganic Biochemistry* 61: 79–96.

Vallejos, X. 1999. Elaboración y evaluación de la calidad de un flan con adición de fibra dietética de nopal. Bachelor's Thesis, Universidad de Chile, Santiago.

Vargas, F. N. 1988. Biología de la cochinilla del carmín *Dactylopius coccus* Costa bajo condiciones de laboratorio en Pampa del Arco (2,750 msnm) Ayacucho. Bachelor's Thesis, Universidad Nacional de San Cristóbal de Huamanga, Ayacucho, Peru.

Velasco, P. H. 1988. Estudio del ciclo biológico de la cochinilla o Grana-cochinilla (*Dacylopius coccus* Costa). Bachelor's Thesis, Universidad Autónoma Chapingo, Chapingo, Mexico.

Vigueras, A. L., and L. Portillo. 1995. Determinación del ácido carmínico en dos generaciones de *Dactylopius coccus* Costa mediante cultivo hidropónico en nopal. *Nakari* 4: 41–48.

Villarreal, P. 1996. Obtención de confitados a base de cladodios de nopal. Bachelor's Thesis, Universidad de Chile. Santiago.

von Elbe, J. H. 1977. Status of colors in dairy products. *Dairy and Ice Cream Field* 160: 60–62.

Wang, C. Y. 1990. Alleviation of chilling injury of horticultural crops. In *Chilling Injury of Horticultural Crops* (C. Y. Wang, ed.). CRC Press, Boca Raton, Florida. Pp. 281–302.

Wouters, J. 1990. Dyestuff analysis of scale insects by high performance liquid chromatography (Homoptera: Coccoidea). In *Proceedings of the Sixth International Symposium of Scale Insect Studies Part II.* Institute of Applied Zoology Agricultural University, Cracow, Poland. Pp. 61–70.

Zambrano, M. L., A. D. Hernández, and Y. Gallardo. 1998. Caracterización fisicoquímica del nopal. In *Fibra Dietética* (F. Lajolo, and E. Wenzel, eds.). Temas en Tecnología de Alimentos, Vol. 2. Instituto Politécnico Nacional, Mexico City. Pp. 29–42.

Zimmerman, H. G., and V. C. Moran. 1991. Biological control of prickly pear, *Opuntia ficus-indica* (Cactaceae), in South Africa. *Agriculture, Ecosystems and Environment* 37: 29–36.

CHAPTER

› 14 ‹

INSECT PESTS AND DISEASES

Helmuth G. Zimmermann and Giovanni Granata

Introduction
Insect Herbivores
Cactus Hosts
Classification of Cactus-Feeding Insects
Host Specificity of Cactus-Feeding Insects
Insect Adaptations to Their Cactus Hosts
Endophagous Herbivores and Survival
External Herbivores
Insect Pests on Cultivated Cacti
Distribution of Pests
Predicting Future Pests
Diseases of Cultivated Cacti
Bacteria
Yeasts
Fungi
Native Fungi on Cacti
Other Diseases
Conclusions and Future Prospects
Literature Cited

Introduction

One of the earliest published records of a cactus-feeding insect dates back to Alexander von Humboldt in 1812 (Ortega 1991), who described how the cochineal insect *Dactylopius coccus* had been cultivated in Mexico and Central America for many centuries before the arrival of Columbus. Between 1877 and 1895, several other publications mentioned insects feeding on cacti in the United States. The most comprehensive work on insects of Cactaceae, published at the beginning of the last century, was *The Principal Cactus Insects of the United States* by Hunter et al. (1912), which lists 324 species, including species from Mexico and Central America, 92 of which are recorded as being injurious to cacti.

Early research into the biological control of alien cactus invaders in countries such as Australia, India, and South Africa made a significant contribution to the study of cactus-feeding insects. Indeed, several cacti, including various species in the genera *Cylindropuntia, Harrisia, Opuntia,* and *Pereskia* from North and South America, have become serious invaders and have been subjected to biological control programs (Dodd 1940; Pettey 1948; Annecke and Moran 1978; Moran and Zimmermann 1984; Julien and Griffiths 1998; Olckers and Hill 1999). As a result, many papers were published on the taxonomy, bi-

ology, and ecology of selected natural enemies used to control these cactus weeds biologically (Blanchard 1922; Cockerell 1929; Dodd 1940; Pettey 1948; De Lotto 1974; Moran and Cobby 1979; Robertson 1987; Robertson and Hoffmann 1989; Hoffmann 1991). Some of these insects are now important pests of cultivated *Opuntia* species.

The most significant research contributions on cactus-feeding insects resulted from the comprehensive surveys made by various entomologists in their search for effective biocontrol agents (e.g., Mann 1969; Zimmermann et al. 1979). These studies focused primarily on the subfamily Opuntioideae (*Cylindropuntia, Opuntia, Tephrocactus*) with some information also on *Pereskia* and *Harrisia* of subfamilies Pereskioideae and Cactoideae, respectively. Very little is known of the insects associated with other genera, particularly those in the Pereskioideae and Cactoideae, because very few of their species have become invaders outside of their natural habitats. The only such species that have become invasive outside the Americas are *Cereus jamacaru, Harrisia martinii,* and *Pereskia aculeata.* Had the whole of the Cactaceae been studied as comprehensively as the Opuntioideae, the number of recorded cactus-feeding insect species would certainly be much larger. Also, the cactus-feeding insects of the Caatinga region of Brazil, as well as those of Paraguay and Bolivia, are undersampled and there are many undescribed species in these regions (Mann 1969). Only limited surveys have been undertaken of the subfamily Pereskioideae, mainly in Argentina (Zimmermann et al. 1979).

Early surveys of cactus pathogens are unknown, most likely because diseases were not considered for biological control of cactus weeds at that stage. The first noteworthy publications on cactus diseases came from North America, where the emphasis was on commercially cultivated ornamentals and native species (Alcorn et al. 1975; Mitchell 1985). Farr et al. (1989) list 10 fungus species causing disease symptoms for *Opuntia ficus-indica.* Most of the important information on cactus diseases is derived from studies of pathogens in the Mediterranean countries, where diseases cause considerable damage to cultivated plantings comprised mainly of *O. ficus-indica* and its many cultivars. Many of the diseases are polyphagous and are well known from other crops. Some, mainly in Mexico, have now spread from native cactus species to those in cultivation.

Insect Herbivores

Cactus Hosts

Compared to other plant families, relatively few cactus-feeding insects have co-evolved with the Cactaceae (Moran 1980). This may be attributed to the unique morphology and physiology of the family. The insects that do feed on succulent Cactaceae usually have co-evolved with their hosts and have special features and adaptations that allow them to survive on these hosts. The main driving force in the evolution of the Cactaceae was the selection for features that reduce desiccation. This resulted in morphological and physiological changes, such as succulence (80–90% water), Crassulacean acid metabolism (CAM; Chapter 4), a large diversity of alkaloids, abundance of oxalic acid, loss of leaves, decreased surface/volume ratios, mucilage, and a tough cuticle (Benson 1982; Barthlott and Hunt 1993). Many cactus-feeding insects have overcome these barriers and have adapted in unique ways to these drastic changes.

The complexity of plants is correlated with the number of insect species associated with them, and the Cactaceae are for the most part architecturally simple—generally no leaves, hairs, or trichomes (Lawton and Schröder 1977; Strong and Levin 1979). These traits, together with the reduced niche space, could have contributed to the reduced but highly host-specific insect fauna observed in the Cactaceae. This is another reason why so few phytophagous insects worldwide have been able to adapt to introduced Cactaceae outside the Americas. In comparison, the evolution of cactus diseases is rapid, because the biochemical characteristics of cactus cells adapt well to the various disease agents' requirements. Thus, epidemics caused by diseases are able to spread rapidly, causing extensive damage to large commercial cactus-pear plantations.

Classification of Cactus-Feeding Insects

In the known cactus-feeding insect community some families, such as the Pyralidae (pyralids) and the Cerambycidae (long-horned beetles), are over-represented, while other important insect families are lacking (Fig. 14.1). The pyralids are most numerous with approximately 58 species feeding on cacti, followed by the cerambycids with 33 species, and the Curculionidae (weevils) with about 20 species. The family Dactylopiidae (cochineals; Chapter 13) is unique to Cactaceae (Fig. 14.1) and all of its nine species are specific to the Opuntioideae, with the exception of *Dactylopius confertus,* which lives on a *Cleistocactus* sp. (De Lotto 1974). The family Cactaceae hosts only one species from the family Diaspididae (scale insects), namely *Diaspis (Diplacaspis) echinocacti;* this species is host specific to the family. The total absence of the large insect families, such as the Noctuidae (noctuid moths) and Pentatomidae (shield bugs), is astonishing, as cacti should be particularly attractive to these insects. The absence of specific and naturally

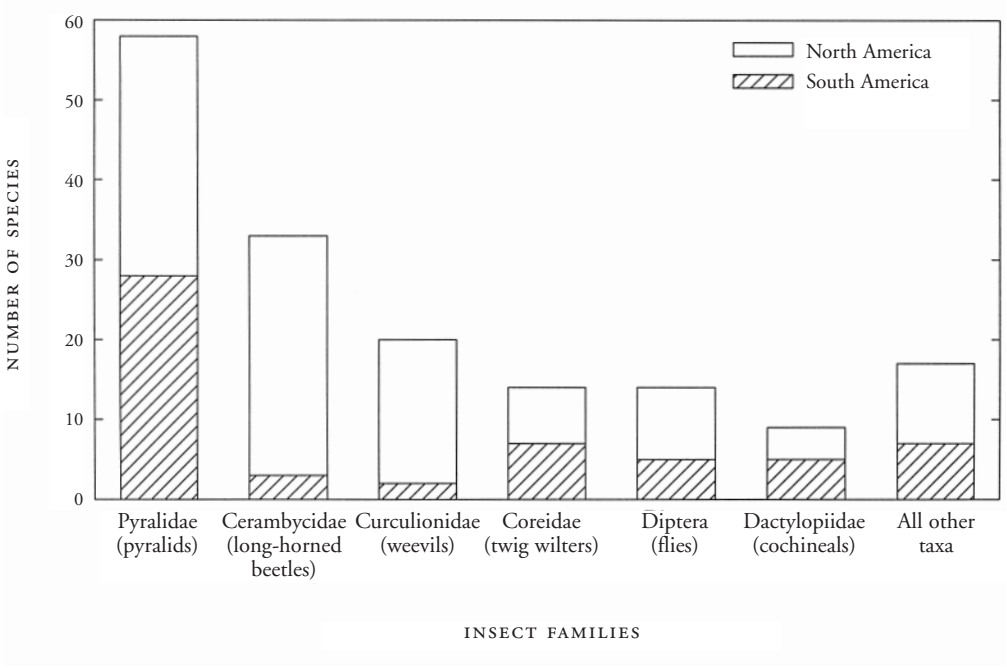


Figure 14.1. The number of cactus-feeding insects in North and South America out of a total of 165 species. Data partially from Moran (1980).

occurring cactus fruit flies (Tephritidae) is equally astonishing in view of the large diversity of fruit found within the Cactaceae. Some of the common fruit flies, which are generalist pests on cultivated fruit worldwide, e.g., *Ceratitis capitata,* have recently switched to *Opuntia* fruit. Moran (1980) showed that, for both North and South America, more insect species feed on the larger opuntias than on the smaller, narrow-jointed ones, which is consistent with the typical species/area relationship of phytophagous insects (Strong 1979).

The differences in the number of insect taxa of North and South American cactus floras suggest a long period of isolation among the cactus-feeding faunas. In particular, very few insect taxa are shared. Second, the large diversity of insects and mites associated with the northern region suggests that most cacti evolved in North America. Specifically, 35% more cactus-feeding species occur in North America than in South America. The small number of curculionid and cerambycid species from South America (Fig. 14.1) is surprising, but more surveys in South America probably will not reveal many more new species that might change this imbalance. The Coreidae (squash bugs) are represented in North America by two large genera, *Chelinidea* and *Narnia,* which are absent from South America. Instead, in South America the Coreidae are represented by the small genus *Leptoglossus,* one of the genera found in both the Americas. The Lonchaeidae (lonchaeid flies) are well represented in South America, as opposed to only two species in North America. Their larvae feed internally in the cladodes of mainly *Opuntia* species.

A fascinating feature of the family Pyralidae is that the larvae of all true cactus-feeding members of the family in South America are reddish, whereas those in North America are blueish, except *Ozamia* and *Sigelgaita,* which vary in color. These aposematic (warning) colors suggest a defense strategy against predators, although which poisonous larvae they mimic is not known. All members of the genera *Ozamia* and *Sigelgaita,* as well as the only species in the genus *Noctuella* in family Pyraustidae (pearl moths), are primarily fruit feeders and occasionally destroy large proportions of fruit (Mann 1969). *Ozamia* species occur in both North and South America, whereas the other two genera are found only in South America. Some of the *Ozamia* fruit-feeding species are associated with a wide host range in both the Opuntioideae and Cactoideae. Because of their ability to consume fruits, it is surprising that these insects are not more serious pests on cultivated *Opuntia* species.

The dominance of internal cladode feeders (Fig. 14.2) within the major insect families associated with Cactaceae may be an indication of the advantages of endophagy. The succulent internal environment, in addition to the tough, thick, wax-covered epidermis typical of the Cactaceae, provides excellent protection. About 75% of all cactus-feeding

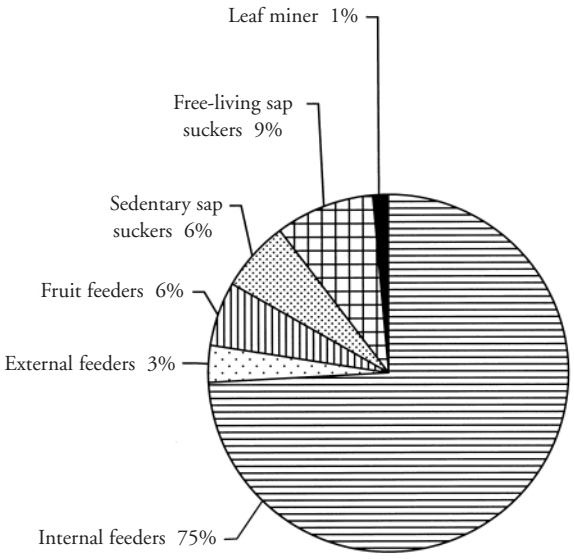


Figure 14.2. Guild structure of the 170 cactus-feeding insects and mites. Some insects fall into more than one category.

insects and mites are internal feeders and only 3% of the species feed externally (Fig. 14.2). The rest are fruit feeders and sap suckers. Even though only a few insects have been collected from the subfamily Pereskioideae (Zimmermann et al. 1979), which contains the primitive, leaf-bearing cactus species, its insect guild differs clearly from that of the other two subfamilies. It is characterized by a higher incidence of external feeders and leaf-miners, which may be attributed to the presence of prominent leaves.

Host Specificity of Cactus-Feeding Insects

According to Mann (1969), about 80% of the species of cactus-feeding insects are found in genera of which all members are restricted to cactus hosts, indicating a high degree of host-plant specialization. On the other hand, within the Cactaceae, very few cactus-feeding insects are monophagous, i.e., restricted to a single host species, such as *Dactylopius salmianus,* which is found only on *Opuntia salmianus.* Most cactus-feeding insects are oligophagous, i.e., restricted to a single genus. A few are restricted to a subfamily. For example, species in the Pyralidae and the Dactylopiidae are mainly associated with the genus *Opuntia* within the Opuntioideae, whereas the Cerambycidae feed on all three subfamilies.

Distinct insect complexes are associated with the sometimes-invoked genera *Platyopuntia* and *Cylindropuntia* of the Opuntioideae, as defined by Backeberg (1976), which might be regarded as evidence in favor of retaining these genera. From western Texas to California, three insects species—the moth borers (Pyralidae) *Cahela ponderosella* and *Alberada parabates,* and the cerambycid *Coenopaeus palmeri*—are all associated with *Cylindropuntia,* including the widely distributed *Opuntia imbricata.* According to Mann (1969), all attempts to rear the two pyralids on *Platyopuntia* were unsuccessful, whereas the cerambycid was able to develop on *Opuntia* species when forced by restrictive cage conditions. Species within the large genus *Narnia* also show very clear preferences for either *Platyopuntia* or *Cylindropuntia,* and the cochineal, *Dactylopius tomentosus,* is associated only with *Cylindropuntia.* Equally, under natural conditions *Cactoblastis cactorum* is only associated with *Platyopuntia,* although under caged condition it can develop on some *Cylindropuntia.* This specificity between insects and host plants can have important implications for cactus taxonomists. It can also be a valuable tool for predicting the future pest status of some of these insects for the large commercial cactus-pear plantations within the insects' native ranges.

Recent studies reveal host-adapted biotypes within certain cactus-feeding insect species. Two distinct, host-adapted biotypes exist in the cochineal *Dactylopius opuntiae.* One of the biotypes attacks only large, tree-like *Opuntia* species, such as *Opuntia ficus-indica,* whereas the other is restricted to low-growing *Opuntia* species, such as the *O. stricta* types in North America (Githure et al. 1999; Volchansky et al. 1999). This implies that certain *Opuntia* weeds can be controlled biologically, using a host-specific cochineal biotype, without threatening the commercial plantations of *O. ficus-indica.* The existence of host-adapted biotypes within the cochineals also has important implications for the biological control of other *Opuntia* weeds. Furthermore, host-adapted biotypes may exist within the commercially cultivated *Dactylopius coccus,* which could have far-reaching consequences for the cochineal industry. In fact, preliminary research suggests that carmine cochineal populations may differ in their host-plant preferences (Robles 1999).

The pyralid moth, *Cactoblastis cactorum* (Fig. 14.3), has a very wide host range within the genus *Opuntia* and has been recorded as developing on at least 29 hosts (Zimmermann et al. 2000). Many of its hosts within the North American opuntias constitute new associations and are being controlled very effectively by *C. cactorum.* Also, the pyralid is able to develop on all six native *Opuntia* species within their native range in Florida (Johnson and Stiling 1998). This spells disaster to many native opuntias in all of mainland North America if the insect arrives there (Zimmermann et al. 2000). The damage caused by *C. cactorum* to cultivated *Opuntia* species in Mexico, should it arrive

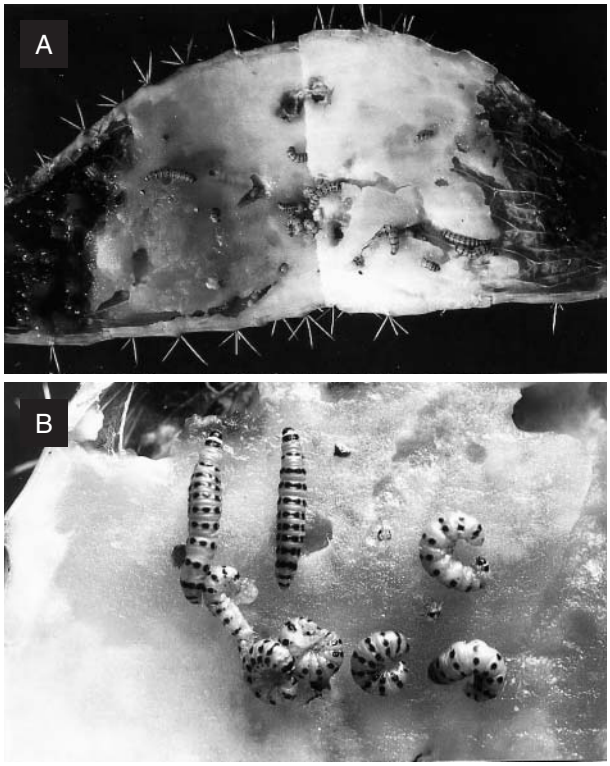


Figure 14.3. Larval stage of *Cactoblastis cactorum:* (A) cross section of infected cladode of *Opuntia ficus-indica;* and (B) close-up of the larvae.

there, could be substantial. In any case, McFadyen (1985) recognized ten biotypes of *C. cactorum,* based on larval differences, host plants, and locality records. Host-adapted biotypes are likely to be found in several other cactus insects, including the Coreidae, e.g., *Narnia* species.

Insect Adaptations to Their Cactus Hosts

Cactus-feeding insects have adapted to the succulence, thick cuticle, and other characteristics that are highly developed within the Cactaceae as adaptations to a xerophytic habitat. These characteristics may explain why insects indigenous to other continents have been unable to adapt successfully to this plant family, members of which have been introduced into those continents as ornamentals, crops, or invaders. The only exceptions are some polyphagous mealybugs, aphids, grasshoppers, and other opportunistic feeders. *Opuntia ficus-indica,* for instance, has been in South Africa for at least 260 years without accumulating any indigenous phytophages, although the time available has certainly been more than adequate and its distribution is wide enough (Moran 1980). More astonishing, none of the native, cactus-feeding insects living on the nearly 160 cactus species in Chile (including one native *Opuntia* species) has permanently switched to the large commercial plantations of *O. ficus-indica* in that country. This indicates that cactus-feeders have a high degree of host specificity, which is rare among other introduced crop plants, as shown in a study of crop plants and their insect pests in South Africa (Moran 1983).

Endophagous Herbivores and Survival

Nearly 80% of all insects feeding on opuntias bore within the succulent plant tissues during the larval stages. This endophagy protects them against predators and parasitoids. The oviposition habits recognized among the cactus-feeding Lepidoptera are also aimed at reducing predation and parasitism, and all show close adaptations to their cactus hosts (Hoffmann and Zimmermann 1989). The most common method, used by the many species in the genera *Cactoblastis* and *Melitara,* entails the female moth depositing her eggs—one on top of the other—in the form of an eggstick that superficially resembles a spine. The larvae hatch simultaneously and enter the cladode collectively through one entrance hole. By entering the cladode more rapidly, the larvae can avoid the mucilage secretions that often repel small larvae (Robertson and Hoffmann 1989). Single, first-instar larvae of *Cactoblastis cactorum* are deterred from penetrating cladodes successfully by the secretions; even if they do manage to enter, it takes longer than when they enter gregariously through a single entrance hole (Hoffmann and Zimmermann 1989). In other pyralids, such as *Tucumania* and members in the Pyraustidae (e.g., *Megastes, Metapleura,* and *Mimorista*), which deposit their eggs singly on thorns or directly on the surface of their hosts, egg mortality is higher than in eggstick-producing species (Hoffmann and Zimmermann 1989). The larvae of all the pyralids are endophagous and are well protected from predators and parasitoids. They are brightly colored in the later instars when they venture out of the cladodes to pupate, suggesting a possible aposematic function. Some members of the Pyralidae are important pests on cultivated *Opuntia* species (Longo and Rapisarda 1995).

Many *Opuntia* species grow in warm, semiarid regions where air and soil temperatures can reach levels of 49°C and 65°C, respectively. For most plants, temperatures over 54°C are lethal, even if they last only a short period (Nobel 1988). Temperatures inside the cladodes of *Opuntia* species are even higher, because lack of daytime stomatal opening associated with CAM prevents water loss and therefore cooling of the surface (Chapter 4). A temperature of 59°C has been measured inside a cladode when the air temperature was only 43°C (Went 1982). How the endophagous pyralid larvae survive these temperatures is not known. In

South Africa, *C. cactorum* larvae have been observed leaving the protection of their cladodes during very hot spells, possibly to avoid the high internal temperatures (Pettey 1948). Such exposure drastically increases the chances for predation.

Carminic acid (Chapter 13) acts as a potent feeding deterrent to parasitoids and ants (Eisner et al. 1980). Nonetheless, two species in the Pyralidae, *Laetilia coccidivora* from North America and *Salambona analamprella* from South America, are uniquely adapted to act as both predators of the cochineals and as phytophages. Their larvae are free-living and tunnel in cladodes underneath cochineal colonies. For self-protection, the larvae of *L. coccidivora* sequester carminic acid from the cochineals on which they prey (Mann 1969; Eisner et al. 1980) and can severely harm the commercial rearing of *Dactylopius coccus* in Mexico (Tito 1998). In any case, sequestering poisons for self-protection is common in insects that feed on poisonous plants.

With the exception of two chrysomelid (leaf beetles) species that feed externally on young cladodes, the larvae of all cactus-feeding species in the Coleoptera (beetles)—notably families Curculionidae and Cerambycidae—are endophagous and thus well protected from parasitoids and predators. Females deposit their eggs individually on the plant in scar tissue or in cracks and crevices, which are then covered with a secretion that hardens to provide protection. The presence of larvae is revealed by frass (debris produced by insects) or gum and/or mucilage exudations. Some of the major pests on cultivated *Opuntia* species are in these two families. The adult cerambycids are all very cryptic and difficult to detect when resting on the bark of their cactus hosts.

External Herbivores

Apart from the polyphagous species in the Miridae (mirid bugs), e.g., *Hesperolabops picta,* all known cactus-feeding sap suckers (Fig. 14.2) in the Heteroptera (bugs) belong to family Coreidae (squash bugs). These are seldom abundant, with the exception of *Chelinidea* species that can develop pest status on cultivated *Opuntia* species in Mexico (Gallegos Vazquez and Mendez Gallegos 2000), causing yellowing around feeding punctures. Most of these sap suckers feed gregariously. At the least disturbance, they move quickly to the protected side of the cladode and with continued disturbance, they drop to the ground to find cover. They are vulnerable to predation and parasitism and have evolved no special protection mechanisms, apart from their rapid movements and the repugnancy typical of coreids.

The most extraordinary insects that have co-evolved with the Cactaceae are the nine species of the genus *Dactylopius* of the Dactylopiidae (cochineals; De Lotto 1974; Chapter 13). They are all sedentary, and the females are protected by a thick waxy covering and the carmine in their body fluids that gives the insect its typical red color. The behavior and life cycles of *Dactylopius austrinus, D. coccus, D. opuntiae,* and *D. tomentosus* have been studied in detail (Dodd 1940; Pettey 1948; Karny 1972; Moran and Cobby 1979; Moran et al. 1982; Hosking 1984; Perez Guerra and Kosztarab 1992; Chapter 13). The insects feed in an exposed position on the surface of the cladodes and are vulnerable to excessive rain, which washes them off the plant. Moran et al. (1987) and Moran and Hoffmann (1987) highlighted adaptations in the insect to avoid excessive damage caused by rain, such as settling in the rain shadow of a cladode or near the protection of a spine. Predators, mainly coccinellid beetles, are well adapted to prey on cochineal in their countries of origin. Predators that have not co-evolved with the insects are less effective due to the deterrent effect of carmine and because of the waxy covering that provides effective protection to the insect (Morrison 1984).

Dactylopius austrinus, D. ceylonicus, D. opuntiae, and *D. tomentosus* have all been used successfully in the biological control of cactus weeds in many countries, and they are rated as one of the most effective groups of biocontrol agents (Zimmermann and Moran 1982; Moran and Zimmermann 1984; Julien and Griffiths 1998). Why these cochineals are so damaging to their hosts is not known. Some of the hosts, e.g., *Opuntia ficus-indica,* can support large populations of *D. coccus* without being obviously affected.

Cactus-feeding insects can apparently detect the CO_2 gradient associated with the plant's CAM activity and use it to their own advantage. The moth *Cactoblastis cactorum* detects small fluctuations in CO_2 around the background atmospheric levels, enabling females to recognize the healthiest and physiologically most active plants (Stange et al. 1995). Cactophagous insects probably have other adaptations to the CAM pathway, such as the effect of the daily acidity fluctuations associated with CAM.

Insect Pests on Cultivated Cacti

Distribution of Pests

Considering the number of recorded cactus-feeding insects and mites, only a few of these species have become pests on cultivated Cactaceae, mainly *Opuntia* species (Longo and Rapisarda 1995). Little is known of the pests of the other

commercially cultivated genera—*Cereus, Hylocereus, Selenicereus,* and *Stenocereus.* By far the largest number of pests are recorded from Mexico, where *Opuntia* species are extensively cultivated (Table 14.1). This is not surprising, as Mexico is home to more than 150 native cactus-feeding insects and also the origin of many cultivated *Opuntia* species (Bravo 1978; Scheinvar 1999). Of the total of 122 specialist *Opuntia*-feeding species listed by Mann (1969) and Zimmermann et al. (1979), only 23 are general pests of cultivated *Opuntia* species in Mexico (Tito 1998; Gallegos Vazquez and Mendez Gallegos 2000).

Very few insect pests have been recorded on cultivated cacti in countries other than Mexico, including the Mediterranean countries. The cactus-feeding pests recorded from southern Africa, Australia, Madagascar, and India (Table 14.1) were deliberately introduced for biological control of *Opuntia* weeds (Moran and Zimmermann 1984; Brutsch and Zimmermann 1995). Except for very polyphagous, opportunistic feeders, such as grasshoppers, aphids, ants, and mealybugs, no record could be found of a permanent host-switch onto cultivated *Opuntia* species from any of the native phytophagous insects in countries outside of North and South America. No insect pests have been recorded from cactus pear in Israel (Y. Mizrahi, personal communication). This is an indication of the taxonomic isolation and the uniqueness of the Cactaceae. Only recently has the introduced Mediterranean fruit fly, *Ceratitis capitata,* been recorded as a pest of fruit of *Opuntia ficus-indica* in South Africa. The only host-specific cactus-feeding insect that has followed the spread of cactus cultivations around the world is the scale insect *Diaspis echinocacti.* Because of the geographical isolation of the Cactaceae, no insect pest of any significance, apart from *D. echinocacti,* has been recorded from Ethiopia, where cactus-pear plantings cover many thousands of hectares along with the large areas of naturalized populations (Behailu and Tegegne 1997).

Opuntia species (Chapter 10) and, to a lesser extent, other species in the genera *Hylocereus, Selenicereus,* and *Stenocereus* (Chapter 11) are widely cultivated in many countries. The insect pests on *Opuntia* species vary considerably, depending on the country and the continent in which they are cultivated (Table 14.1). The pests in these countries will be divided into three geographic areas, beginning with North and South America. Countries in these regions, especially in North America, have the highest diversity of insect pests. These are native species that have transferred to cultivations and differ from North to South America. In Argentina, *Cactoblastis cactorum* is by far the most serious pest (Ochoa de Cornelli et al. 1992), but it is absent from Brazil (Pernambuco) because of slow dispersal from its native range in Argentina, Uruguay, and Paraguay (G. P. de Arruda, personal communication). Many major pests are found in Mexico (Table 14.1), including *Anastrepha* species (Tephritidae), *Cactophagus (Metamasius)* species (Curculionidae), *Chelinidea* species (Coreidae), *Cylindrocoptorus* species (Curculionidae), *Dactylopius* species (Dactylopiidae), *Olycella* and *Laniifera* species (Pyralidae), and *Sericothrips* species (Thripidae; Gallegos Vazquez and Mendez Gallegos 2000). Several minor pests are also present.

The second area includes southern Africa, Mauritius, Australia, India, and some West Indian islands (Table 14.1). These are countries that have deliberately introduced *Cactoblastis cactorum, Dactylopius opuntiae,* and other insect species (Julien and Griffiths 1998) for the biological control of various *Opuntia* weeds (Moran and Zimmermann 1984). In most cases, the control is successful. The former two insects are now pests on cultivated *O. ficus-indica* and its cultivars, and control measures against them are necessary for successful cultivation of cactus pear (Annecke et al. 1976). The host-specific mealybug (Pseudococcidae) *Hypogeococcus festerianus* and the cerambycid beetle *Alcidion cereicola* were introduced into Australia and South Africa for the biological control of *Harrisia martinii* and *Cereus jamacaru* (Julien and Griffiths 1998). Both of these insect species will become pests should these countries decide to develop *C. jamacaru* as a commercial crop, as is the case in Israel (Mizrahi and Nerd 1999). Although the curculionid beetle *Cactophagus (Metamasius) spinolae* has been released as a biocontrol agent against *O. ficus-indica* in South Africa and is now well established and effective at one locality in the Eastern Cape, it has not yet dispersed to cultivated plantations of *O. ficus-indica.* This insect has the potential to become a serious pest on cultivated cactus pear plantations in South Africa.

Mediterranean countries, Ethiopia, the Canary Islands, Iran, and Iraq have very few pests on cultivated *Opuntia* species (Longo and Rapisarda 1995; Table 14.1). First, the pests were not transferred together with the plants at the time of introduction from their countries of origin; second, these countries had no biological control projects against invading *Opuntia* species; and third, no native insects transferred to *Opuntia* hosts. Some opportunistic feeders are occasionally found causing temporary damage to plants in these countries. The cactus scale insect, *Diaspis echinocacti,* is the only insect that followed the introductions of *Opuntia* species throughout the world and is now found wherever such species are grown. A noncactus pest that has recently started causing damage to cultivated fruit in many countries, including South Africa and those in the

TABLE 14.1
Insect pests on cultivated *Opuntia* species for various geographical areas

Insect order and species	Pest status	Distribution	Remarks
		North and South America	
Lepidoptera			
Cactoblastis cactorum	Unknown	Florida, Mexico?	Accidental arrival in Florida attacking native species; occurrence in Mexico unconfirmed; South American origin
	Severe	Argentina	Gregarious internal feeder; native transfer
Megastes cyclades	Severe	Mexico, USA	Gregarious internal feeder; native transfer
(Laniifera cyclades)			
Olycella nephelepasa	Sporadic	Mexico	Solitary internal feeder; native transfer
O. subumbrella	Sporadic	Mexico	"
O. junctolineella	Sporadic	Mexico	"
Sigelgaita chilensis?	Uncommon	Chile	Cladode and fruit feeder; native transfer
Coleoptera			
Cactophagus spinolae	Severe	Mexico, USA	Stem borer; native transfer; prefers large species
(Metamasius spinolae)			
C. fahraei (Metamasius fahraei)	Sporadic	Mexico	Stem borer; native transfer
Cylindrocopturus biradiatus	Sporadic	Mexico	Solitary cladode borer; native transfer
C. ganglbauberi	Sporadic	Mexico	"
Moneilema variolare	Sporadic	Mexico	Solitary stem borer; native transfer
Hemiptera			
Chelinidea tabulata	Severe	Mexico, USA	External sap suckers; native transfer
C. vittiger	Sporadic	Mexico, USA	"
Narnia femorata	Sporadic	Mexico	"
Homoptera			
Dactylopius ceylonicus	Uncommon	Argentina	Native transfer; taxonomy unclear, needs verification
D. opuntiae	Severe	Mexico, USA	External sap suckers; native transfer
Diaspis echinocacti	Sporadic	North America	Scale insect; wide distribution
(Diplacaspis echinocacti)	Sporadic	All countries	Native transfer; subject to biological control
Diptera			
Anastrepha sp.	Sporadic	Mexico	General fruit pest; non-specific
Asphondylia opuntiae	Sporadic	Mexico, USA	Fruit feeder; native transfer
Dasiops bennetti	Rare	Mexico	Internal cladode feeder; native transfer
Thysanoptera			
Sericothrips opuntiae	Common	Mexico, USA	External sap suckers; discolors cladodes; native transfer
Acari			
Tetranychus opuntiae	Common	Mexico, USA	External sap suckers; native transfer

Mediterranean region, is the Mediterranean fruit fly, *Ceratitis capitata* (Longo and Rapisarda 1995).

Predicting Future Pests

With increasing globalization and the introduction of cactus pear as a commercial fruit and fodder plant into many countries, many pests will eventually find their way to new countries and continents, with potentially disastrous consequences to local cactus-pear industries. Crawlers of *Dactylopius* species can be dispersed over long distances by the wind (Moran et al. 1982). As increased cultivation provides more targets for the pests, their chances of locating these targets will improve considerably. Once *Dactylopius opuntiae* has reached any of the Mediterranean countries in

TABLE 14.1 (*continued*)

Insect order and species	Pest status	Distribution	Remarks
Southern Africa, East Africa, Mauritius, Australia, India, and some smaller islands			
Lepidoptera			
Cactoblastis cactorum	Severe	Southern Africa, Australia, Cayman, Nevis, Montserrat	Introduced for biological control of *Opuntia* weeds; origin Argentina via Australia and South Africa
Coleoptera			
Cactophagus spinolae (*Metamasius spinolae*)	Negligible	South Africa	Introduced from Mexico for the biological control of *Opuntia ficus-indica*; very localized and still absent from cultivations
Homoptera			
Dactylopius opuntiae	Severe	Southern Africa, Eastern Africa, India, Mauritius, Madagascar	Introduced from Mexico for the biological control of various *Opuntia* weeds
Diaspis echinocacti (*Diplacaspis echinocacti*)	Sporadic	All countries	Original from the Americas
Diptera			
Ceratitis capitata	New	South Africa	Cosmopolitan fruit fly transferred to *Opuntia* fruit
Mediterranean Countries, Ethiopia, Middle East			
Homoptera			
Diaspis echinocacti (*Diplacaspis echinocacti*)	Sporadic	All countries	Original from the Americas
Pseudococcus spp.	Sporadic	All countries	Polyphagous pest and common on ornamental cacti
Diptera			
Caratitis capitata	Sporadic	Most countries except Ethiopia	Cosmopolitan fruit fly; transferred to *Opuntia* fruit

which cactus pear is cultivated, it is likely to spread effectively throughout the region. Presently, cactus pear cannot be cultivated in South Africa on a large scale without the interference of this cochineal, due to the insect's effective dispersal abilities. Figure 14.4 shows countries into which *Dactylopius opuntiae* has been introduced intentionally for the biological control of *Opuntia* weeds. These countries now serve as focal points for the further spread of the insect.

The movement of certain other cactus-feeding insects for biological control purposes also decreases their distance from new targets. Some of these insects have the potential to become serious pests on cultivated opuntias and may also threaten native *Opuntia* species. The recent dispersal of *Cactoblastis cactorum* within the West Indies and eventually to mainland Florida, either through inadvertent introductions by the nursery trade (Pemberton 1995) or through natural dispersal, has serious consequences for both the native *Opuntia* flora and cultivated plants in the United States and Mexico (Zimmermann and Perez-Sandi y Cuen 1999). Figure 14.5 shows the history of the introduction and spread of *C. cactorum* from Argentina since 1925. The many interceptions at the main entry points into the southeastern United States of cactus plants containing endophagous *C. cactorum* larvae and belonging to the cactus nursery trade demonstrates how easily the insect's entry into the country might pass unobserved (Pemberton 1995). A lively cactus trade also exists between Europe and many American countries, and the arrival of the insect into Mediterranean countries is therefore almost inevitable.

In the state of Pernambuco, Brazil, cultivated *Opuntia* species are important as a source of fodder, and about

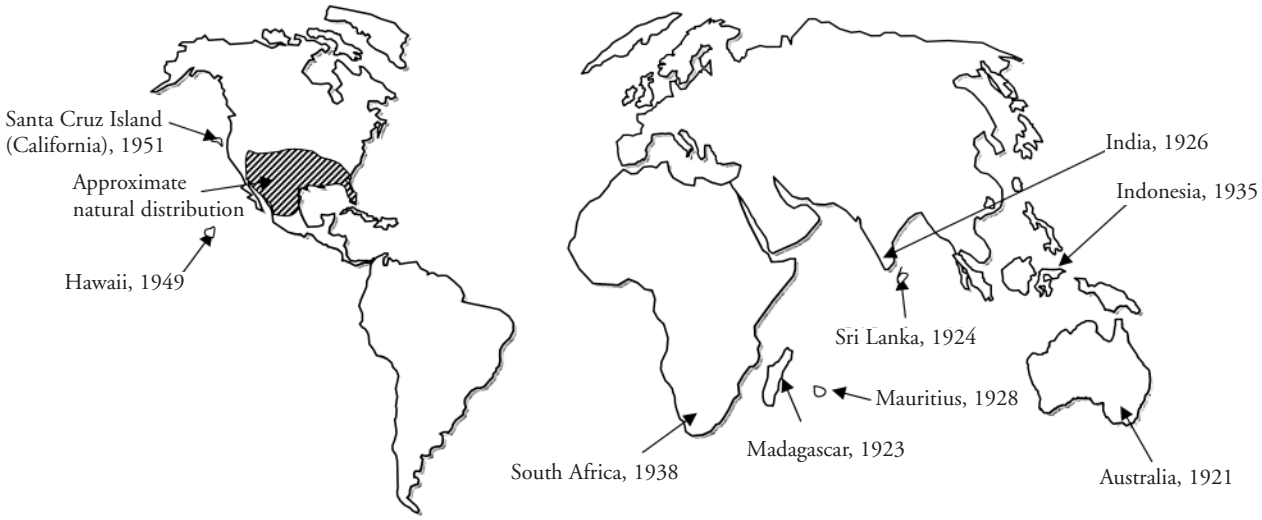


Figure 14.4. Countries where *Dactylopius opuntiae* has been intentionally released for the biological control of *Opuntia* weeds.

400,000 ha are under cultivation (Barbera 1995). This can provide an easy target for both *C. cactorum* from the south and *Dactylopius opuntiae* from the north. Increased cultivation of cactus pear between Paraguay and Pernambuco will eventually form a host chain that might allow *C. cactorum* to spread naturally to these areas. The Andes form a natural barrier between the *Opuntia* species infested with *C. cactorum* in Argentina and the pest-free cultivations in Chile but, with increasing cultivation of *O. ficus-indica* in some Andean valleys in Argentina, these distances have decreased considerably. Within Africa, both *C. cactorum* and *D. opuntiae* may disperse northward from Zimbabwe via Kenya to Ethiopia because the cultivation of *O. ficus-indica* in the arid zones between these two countries is being encouraged.

Little is known of the dispersal behavior of the other major cactus pear pests in Mexico. However, with the increasing cactus trade and the large number of amateur cactus collectors moving cacti between countries and continents, the inadvertent dispersal of new insect pests is inevitable.

Diseases of Cultivated Cacti

The most important cactus pear diseases can be grouped according to their pathogenic agents (Table 14.2). The biotic diseases are caused by bacteria, yeasts, fungi, phytoplasmas, viruses, and some not-so-well-defined agents called phytoplasma/virus-like organisms. Some diseases and disease-like symptoms on cactus pear can also be caused by abiotic conditions, e.g., environmental stress (such as hailstorms), genetic anomalies, incorrect pesticide application, and physiological disorders. Biotic diseases of cactus pear are present in all the growing areas. They are influenced by the presence of the pathogen as well as climatic conditions. For example, bacterial diseases are more prevalent in Chile, Argentina, Mexico, and Italy than in Peru and North Africa because the elevated temperatures and low humidity in the latter two regions do not favor this type of disease. Although fungal diseases are also influenced by environmental conditions, some have not been reported in certain countries, probably because the pathogen is not present in that region. For example, *Alternaria* golden spot is present and causes severe damage in Mexico, Italy, and South Africa but not in other cactus-pear growing countries; *Aecidium* spp. provokes major disease only in Peru; *Cercospora* spp. is prevalent in Peru and Bolivia; *Phoma sorghina* causes damage only in Argentina; and *Dothiorella ribis,* the causal agent of a cactus-pear gum cancer, has been found only on the small island of Linosa (Italy). Few systematic studies have focused on cactus pear viral diseases, even though various reports exist (Chessin 1965).

The evolution of cactus diseases is very rapid, as the biochemical characteristics of the cell juices adapt well to the various biotic agents' requirements. This extremely important fact should highlight the urgency of preventing diffusion of diseases that can rapidly become epidemic. Strict control must be performed on propagation material. Prevention is the best approach to guarantee successful cultivation of cacti, and propagation material and fruit should not be imported from areas where specific diseases are present.

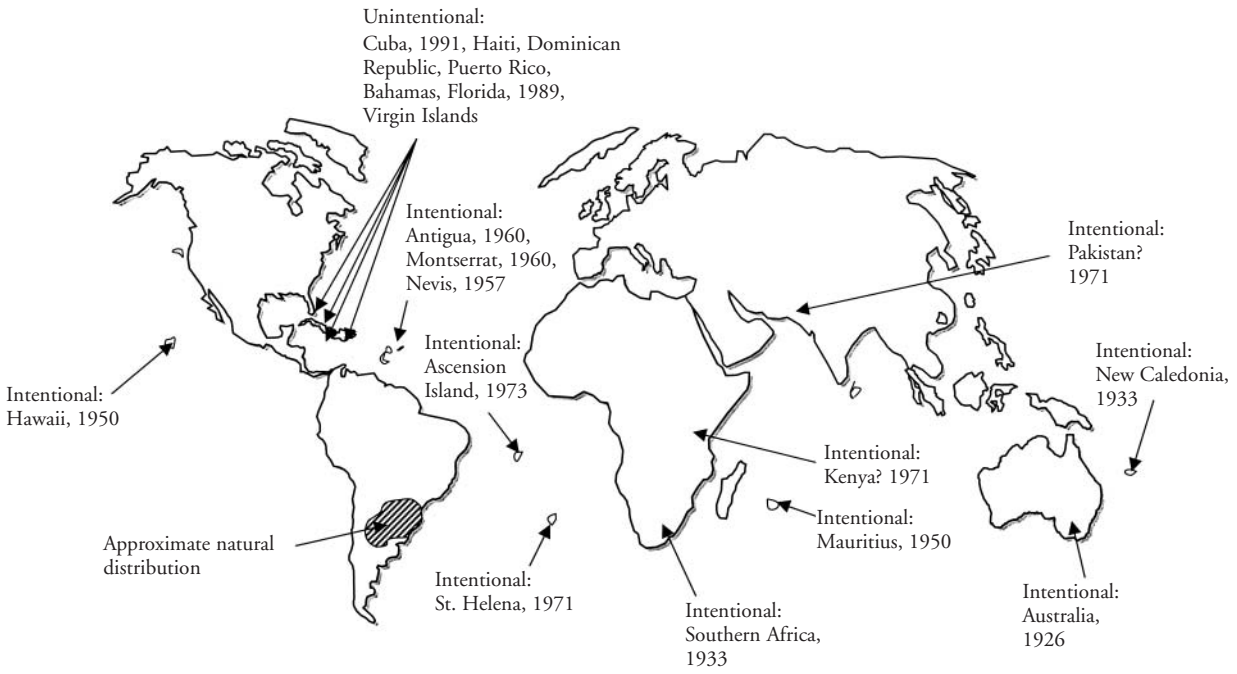


Figure 14.5. Intentional and unintentional introduction of *Cactoblastis cactorum.* Establishment in Kenya and Pakistan is not confirmed.

Bacteria

Cactus pear tissues have a relatively high water content and therefore infections, especially bacterial infections, rapidly turn into rot (Table 14.2). Saprophitic colonization occurs, which makes it difficult to isolate the pathogenic agent. Bacteria are prokaryotes. About a hundred species lead to plant and animal diseases (Bradbury 1970; Buchanan and Gibbons 1974). The most common pathogenic genera of bacteria are *Agrobacterium, Corynebacterium, Erwinia, Pseudonomas,* and *Xanthomonas* (Skerman et al. 1980; Krieg 1984).

Bacterial agents do not possess penetrating mechanisms and can only access plants through wounds. Infection requires specific weather conditions characterized by low temperatures and elevated atmospheric humidity plus the presence of a film of water on the plant tissues. Consequently, bacterial diseases are more widespread in moist regions or during wetter times of the year. Bacteria-induced symptoms are caused by cell death (necrosis) and sometimes abnormal growth (tumors) of the infected organs due to hyperplasia (abnormal cell multiplication) or hypertrophy (abnormal cell size), and they generally result in soft rots in the Cactaceae (Lelliott and Stead 1987).

Bacterial spot has been reported from India, Italy, and certain other cactus-pear growing countries (Argentina, Chile, and Mexico). It is the most severe cactus pear dis-

TABLE 14.2
Biotic pathogenic agents of cactus pear diseases

Bacterial Diseases
Bacterial spot (*Erwinia carotovora, E. cacticida*)
Crown gall (*Agrobacterium tumefaciens*)
Yeast Diseases
Soft rot (*Candida boidimi*)
Fungal Diseases
Armillaria rot (*Armillaria mellea*)
Alternaria golden spot (*Alternaria alternata*)
Foot rot (*Phytophthora cactorum, P. nicotianae*)
Gray mold (*Botrytis cinerea*)
Other fungal agents: *Aecidium* sp., *Cercospora* sp., *Colletotricum* sp., *Cytospora* sp., *Hansfordia* sp., *Fusarium oxysporum*, *Gleosporium herbarum*, *Mycospherella* sp., *Phoma sorghina*, *Phyllosticta opuntiae*, *Phyllosticta concava*, *Pleospora herbarum*, *Sclerotinia sclerotiorum*
Phytoplasmalike and Viruslike Diseases
Cladode enlargement
Flower proliferation

ease in areas where winter or spring frosts and hailstorms wound cladodes or fruits. High summer temperatures arrest the infection, but the bacterium (*Erwina* species) becomes active as soon as cooler, moist conditions prevail (Cortés and Fucikovsky 1986; Alcorn and Orum 1988; Fucikovoky 1990; Granata and Varvaro 1990; Varvaro et al. 1993). The main pathogenic organism of bacterial spot is *Erwinia carotovora* (Table 14.2), which is rod-shaped, gram-negative, motile by perytrichois flagella, and aerobic. This bacterium grows at temperatures up to 36°C, but the optimal temperature is 10 to 15°C. In addition to cactus pear, it can also infect other species of *Opuntia.* Symptoms appear on the cladodes in the spring and consist of translucent spots that coalesce, darken, and eventually turn black. Parenchymatous tissues under the integument are initially water-soaked and then turn brown to nearly black. The superficial infected tissues dry, develop into a scab, and are frequently cracked (Fig. 14.6A). To control the disease, the infected cladodes must be removed. They must not be buried in the plantation area and burning is recommended. Two copper-based fungicide applications are recommended in the winter-spring where the disease is widespread and after hailstorms or other events that cause plant wounds. In Mexico the black soft rot on cactus pear is caused by *Erwinia cacticida* and coffee rot is caused by *Erwinia carotovora* subsp. *atrospetica* (Hernandez et al. 1997)

Crown gall is another bacterial disease that occurs on cactus pear in Mexico under the name "Agalla del Nopal" (Gutiérrez 1992) and is present worldwide. The pathogenic agent is *Agrobacterium tumefaciens* (Table 14.2), which affects diverse species of plants. It lives in the soil as a saprophyte and colonizes the upper roots and the crown of a plant. Symptoms consist of tumoral masses at the base of the stem. The tumors can become 10 cm in diameter, are dark in color, and are cracked when mature. A dark amber exudate, which oozes from the stem near the tumor, can be mistaken for fungal infections. In reality, the tumor does not substantially damage the plant, but it should still be removed and destroyed. Copper-solution treatments can control the disease, and wound closure using gum mastic is recommended.

Yeasts

Yeasts are larger than bacteria and possess some morphologic and structural features placing them between bacteria and other fungi (Lodder 1974; Kreger 1984). They are single-celled organisms and, unlike bacteria, are eukaryotes (possess a nucleus) and can develop under both aerobic and anaerobic conditions. Yeasts respire and promote fermentation utilizing monosaccharide sugars, i.e., sugars with six carbon atoms that often derive from disaccharides (e.g., sucrose) cleaved by enzymes. Yeasts attack plants that have been debilitated by fungal or bacterial infection; they are more destructive than bacteria, as fermentation eventually kills the entire infected organ.

The yeast disease cladode soft rot (Fig. 14.6B) is frequently associated with bacterial spot (Phaff et al. 1978, 1985; Starmer et al. 1978; Granata and Varvaro 1990). The pathogenic agent, *Candida boidimi* (Table 14.2), is most active at temperatures between 20 and 35°C. The initial symptoms are black areas caused by internal tissue infection on the cladodes and fruits, followed by internal tissue rot, after which the plant becomes a deliquescent mass. The entire cladode surface blackens, but the external tissue does not rot and thus the cladodes resemble a limp handbag containing a foul-smelling liquid. Control is most effective when the infected cladodes are removed and destroyed followed by a 1% Bordeaux mixture treatment. Treatments used against bacterial diseases, such as bacterial spot, are also efficacious.

Fungi

Fungi cause both plant and animal diseases. To date about 100,000 species of fungi have been studied and over 800 possess more or less virulent plant pathogenic action. Fungal infections cause physiological alterations in host plant transpiration, respiration, and nutrition and lead to damage ranging from stunted growth and production to death of the whole plant, or part thereof. Indeed, fungi are the most common pathogenic agents in the plant world, including the Cactaceae. Characterized by a vegetative stage made up of mycelium (hyphae) that ensures fungal growth, fungi have a parasitic relationship with the host plant. Hyphae produce spores by agamic processeses or conidia. Spores and conidia are propagation forms that enable fungal diffusion in the environment. When they come into contact with receptive hosts under suitable environmental conditions, they germinate and produce hyphae, some of which penetrate intact surfaces or access the plant through natural openings, e.g., stomata or wounds. As previously noted, cacti have few natural openings and a tough waxy epidermis, thus pathogenic agents rarely penetrate the skin and cell wall; however, they are vulnerable to pathogenic attack through wounds. Fungal diseases can be diagnosed by typical symptoms and microscopic examination of the structure and reproductive bodies of the fungus on the colonized organs or in artificial media (Agrios 1978).

Armillaria root and stem rot (Table 14.2) is a slowly progressing disease that leads to the death of a plant. It is caused by *Armillaria mellea,* a basidiomycetous fungus that

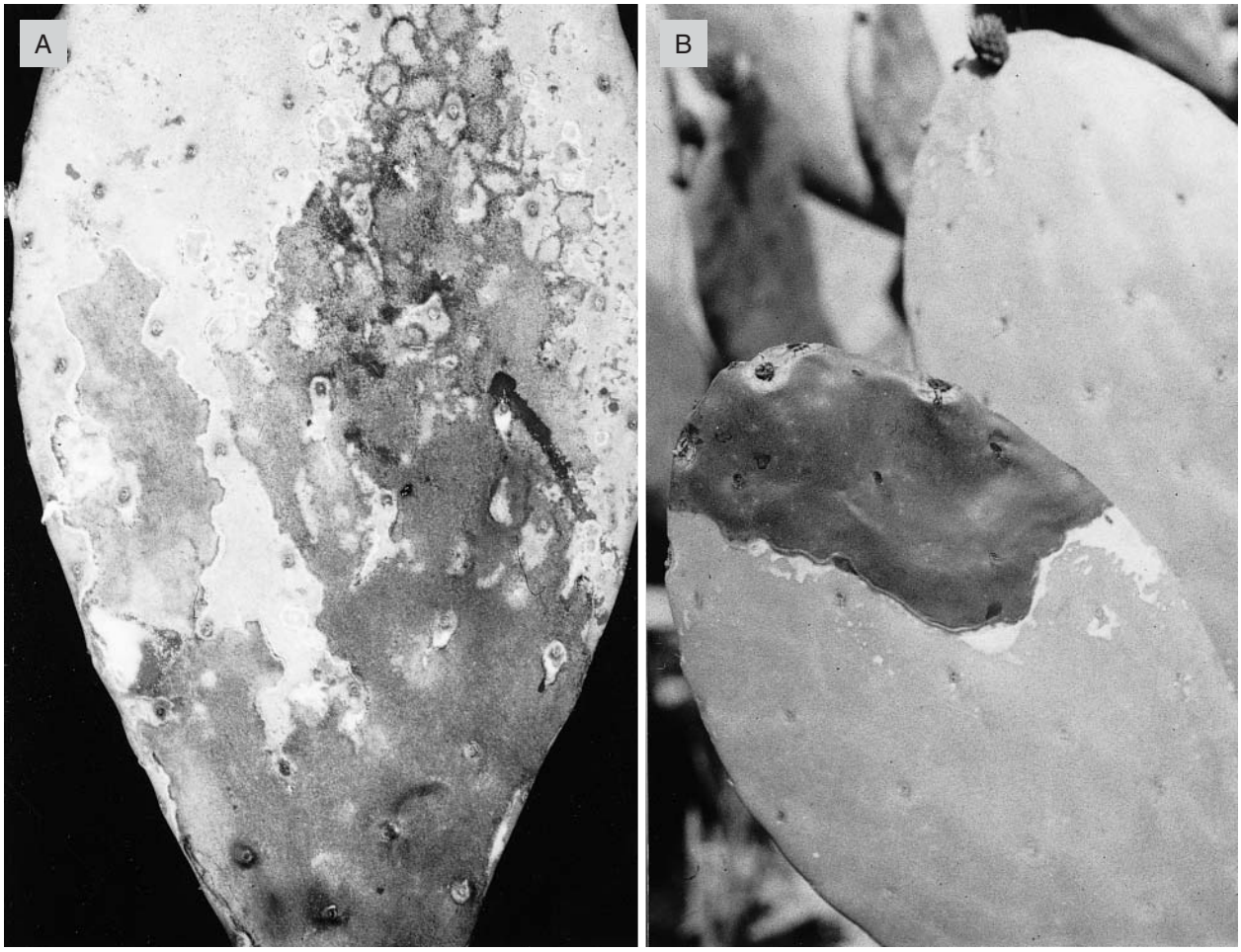


Figure 14.6. (A) Cladode of *Opuntia ficus-indica* with symptoms of bacterial spot and (B) dark areas of cladode caused by the yeast disease, soft rot.

colonizes the shoot and main roots of the plant and produces white mycelium and cordons of hyphae that spread from the infected tissues and contaminate neighboring plants. The presence of hyaline, elliptical, and smooth basidiospores produced by carpophores are characteristic of infections caused by this disease. Infected plants suffer a decline in tissue turgor and chlorosis resulting from phloem disorganization and altered water and mineral nutrition. Fruits borne by the infected plant are small and do not ripen. The infected tissue at the stem base eventually rots and releases a viscous exudate. A white mycelium emitting a characteristic fungus smell is found under the bark. The contaminated portion of the shoot has a bright-red border (Redfern 1968, 1973; Raabe 1979; Mangano di San Lio and Tirrò 1983). This fungus is ubiquitous, polyphagous, and often remains in the soil in residues from previous cultivations, thus inevitably infecting new crops. It is advisable not to cultivate *Armillaria*-infected soil for 2 or 3 years and to remove sources of inoculum (roots of previous cultures). Effective chemical control of the disease is not yet available.

Alternaria golden spot (Fig. 14.7A) has been reported in Mexico under the name of "Mancha de Oro" and is also present in Italy and South Africa. It is caused by the fungus *Alternaria alternata* (Table 14.2) that generally penetrates the plant near the spines of cladodes. A slightly raised round spot appears close to the site of penetration; the underlying tissue then changes from dark to light green and the spot becomes golden. Spots can also appear on the fruits. Spraying with a copper- or Captan-based fungicide can be an effective control for this disease. Ideally, treatment should be applied to potentially vulnerable plants prior to the onset of the symptoms.

Phytophthora cactorum (Fig. 14.7B) and *P. nicotianae* are the pathogenic agents of foot rot (Table 14.2) and are found in cultivations of cactus pear and other Cactaceae (Cacciola and Magnano di San Lio 1988). These fungi live in the soil and usually attack the plant shoot and roots, es-

pecially in irrigated areas where surface water is present. Gum begins to ooze from the stem base of infected plants at the end of the spring, exuding the greatest amounts during the summer. Diseased innermost tissues rot and turn reddish. The rot may involve the entire stem circumference and kill the plant. Infected plants become chlorotic, growth slows, and cladodes wilt, causing the plant to fall over. Clay soils where water stagnates are prone to infection with *Phytophthora* species. Thus, cactus pear should be cultivated in sandy soils, and applications of specific fungicides are recommended wherever this disease prevails.

Gray mold of cactus pear fruits is caused by the fungus *Botrytis cinerea* (Fig. 14.8A). It can start anywhere on the plant, but it generally begins in wounds caused when removing fruits from the cladodes. The infected areas are usually gray and round. When peeled, the underlying fruit tissues appear decayed and soft. The infection spreads in hot humid areas, with the entire fruit becoming a soft, decaying mass. Typical green or blue colonies of *Penicillium* are often observed on the diseased fruit surface (Fig. 14.8A). Gray mold is difficult to control on cactus pear fruits, as the spines and glochids on fruits cause wounds that promote infection during harvesting and processing.

Cactus pear is host to many other fungi that can cause damage under particular environmental and host conditions. *Aecidium* species induces the disease called "Roya" in Peru, leading to small chlorotic spots on the cladodes and fruits in the early summer; the spots enlarge and give rise to pustules with orange-colored centers that deform the fruit. Infected fruit do not ripen fully. *Cercospora* spp. induce circular (1.0–1.5 cm diameter) necrotic wounds on the cladodes (Fig. 14.8B) and fruits and is the most serious cactus disease in Peru and Bolivia. In Mexico *Colletotricum* spp. cause dark brown spots with reddish tints that generally start at the edges and then extend over the entire cladode or fruit. *Cytospora* spp., *Gleosporium* spp., *Mycospherella* spp., *Phoma sorghina* (Fig. 14.8C), and *Pleospora herbarum* also produce necrotic spots on cactus pear cladodes and are found in various countries. *Fusarium oxisporum* f.s. *opuntiarum,* the causal agent of "Fusarium wilt," affects the vascular tissues and causes wilting of cladodes and fruit, leading to a reddening of infected tissues. *Phyllostica concava* and *Phyllostica opuntiae* occur in Mediterranean areas and Mexico, respectively, and produce small, round, rust-colored "scabies" for cactus pear; the fungal fructifications appear as black spots. A *Phyllostica* species is also causing damage to *Opuntia ficus-indica* cultivated in Argentina (Wright 1997). *Sclerotinia sclerotiorum* causes a cottony rot on cladodes of cultivated cactus pear in Chile and on native *Opuntia* species in Argentina. The cuticle softens, the contaminated tissue then darkens, flakes off, and is covered with white wool; soon numerous black sclerotia appear from the decayed tissues. *Hansfordia* species are other fungi found in Mexico that cause black spots (Hernandez 1992).

Native Fungi on Cacti

Very few surveys have been made of native cactus diseases within North and South America. South African pathologists have surveyed for potential pathogens to be used for the biological control of jointed cactus, *Opuntia aurantiaca* (Moran and Annecke 1979; Mildenhall et al. 1987). Some of these diseases may switch to cultivated *Opuntia* species once the areas under cultivation in the Americas and elsewhere increases. The most prominent diseases within native *Opuntia* species are *Aureobasidium pullulans, Fusarium proliferatum,* and *Microdochium lunatum* (Mildenhall et al. 1987). The latter disease already occurs widely on native and cultivated *Opuntia* species in Argentina, the southwestern United States, South Africa, Australia (Dodd 1940), and the Canary Islands (Von Arx 1984), and on *Opuntia ficus-indica* in Spain (Wollenweber and Reinking 1935). This disease was studied in South Africa as a potential biocontrol agent against *O. aurantiaca* (Witbooi 1991). The disease forms circular necrotic spots that eventually collapse and fall out, leaving a clear circular opening. Under certain conditions, the fungus can cause rotting of entire cladodes.

Other Diseases

A disease leading to cladode enlargement has been reported in Mexico under the name of "*Engrosamiento excesivo de cladodios*" and can occasionally develop into a serious problem for cactus pear cultivation in that country (Pimienta-Barrios 1974; Gutierrez 1992); the causal agent is unknown (Hernandez 1992). The characteristic symptoms of this disease are stunted plant growth, followed by cladode swelling and gradual loss of the plant's green color. Flower production is reduced and flowers generally form on the flat part of the cladodes, whereas on healthy cladodes flowers form on the upper edge. Fruit production is poor in terms of both number and weight. Cladodes from vigorous, healthy plants should be chosen for planting. During the first years, any plants manifesting the symptoms of cladode enlargement in new cactus-pear plantations should be removed and replaced with healthy ones. In old plantations, infected plants must be eliminated and destroyed.

Flower proliferation is a cactus-pear disorder that has been encountered only in Mexico, on a limited number of natural and cultivated varieties. The disease is spreading in Mexico and could pose serious damage to cactus-pear cultivations if not controlled by selection. This disease is char-

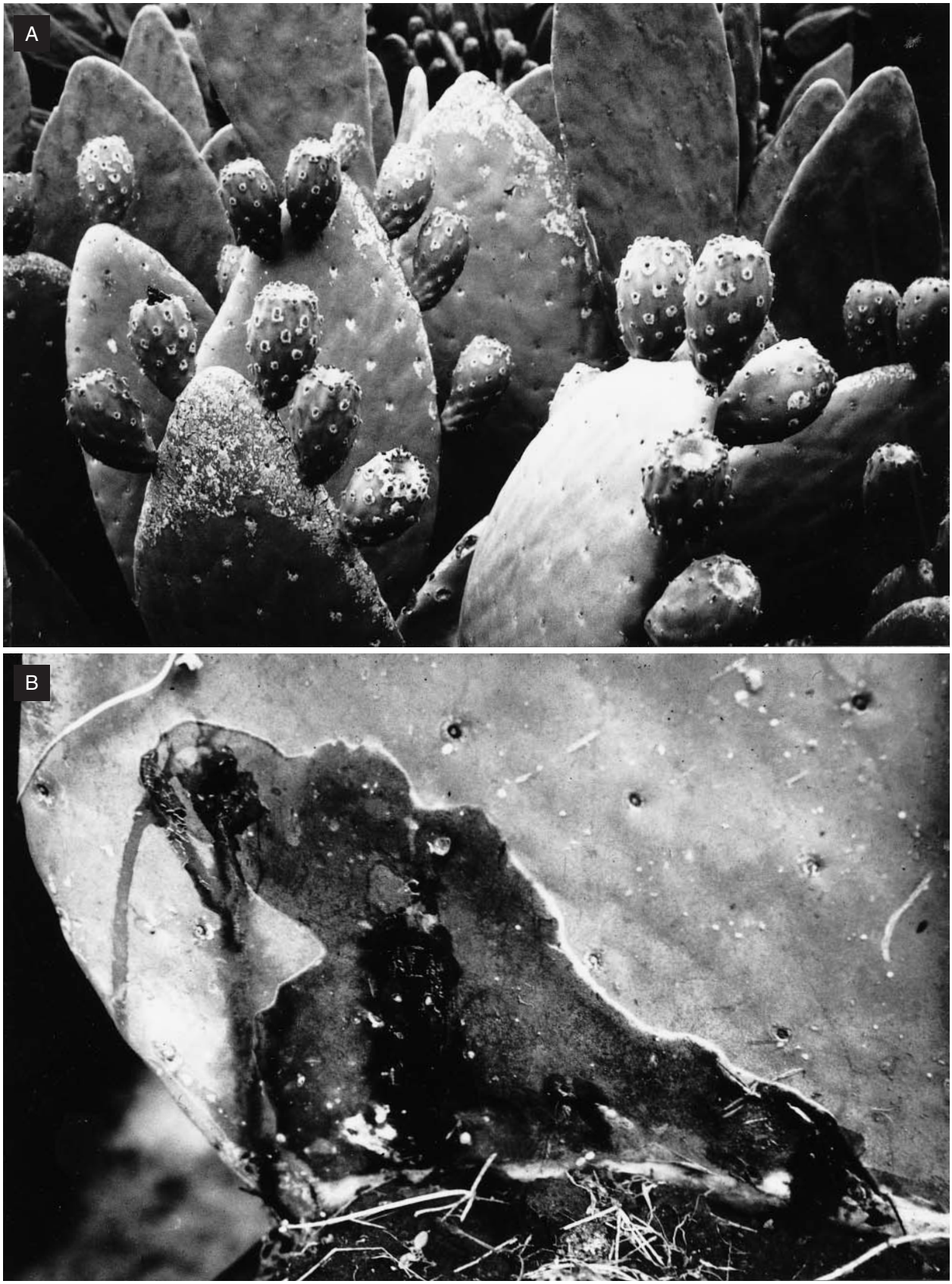


Figure 14.7. (A) Cladodes and fruits infected with *Alternaria* golden spot and (B) foot rot caused by *Phytophora cactorum*.

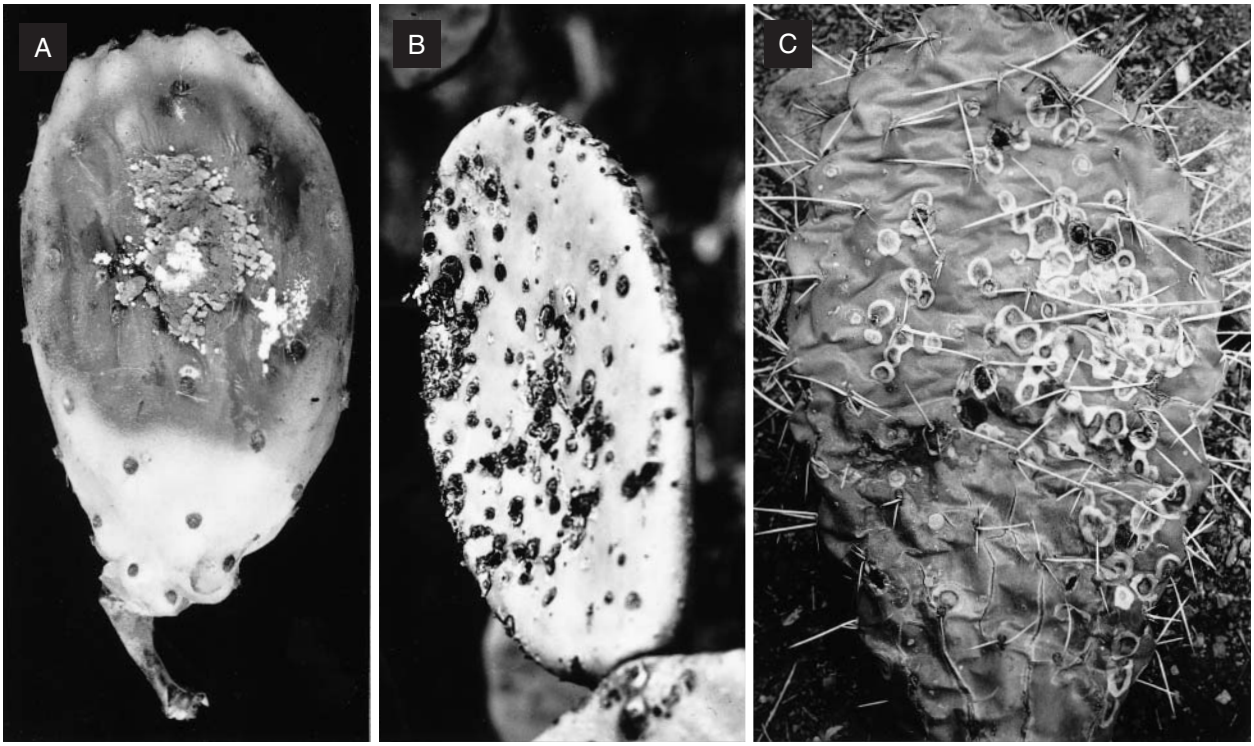


Figure 14.8. (A) Gray mold caused by *Botrytis cinerea* on fruit, with secondary fungus *Penicillium* sp.; (B) cladode infected by *Cercospora;* and (C) necrotic spots caused by *Phoma sorghina.*

acterized by excessive flower production all over the cladode surface, early detachment of flowers (receptacles), and premature spine abscission. The young cladodes are deformed, and new fruits may differentiate from the upper part of fruits. Finally, some phytoplasma and virus-like cactus pear diseases can be transmitted by grafting but the pathogenic agents are not known. The microorganisms involved cause alterations in the phloem and consequent stunted plant growth, yellowing, and low productivity.

Conclusions and Future Prospects

The cactus-feeding insects associated with subfamily Opuntioideae are well documented, but those associated with the other subfamilies, Cactoideae and Pereskioideae, are little known and need further study, particularly in some South American countries. The known insect guild is characterized by a high degree of specificity and unique adaptations to the Cactaceae. The insect families Pyralidae, Cerambycidae, and Curculionidae dominate the guild, and all their cactus-feeding species are endophagous. Of the nine species in the Dactylopiidae, which are all associated with Cactaceae, four species have become well known as highly successful biological control agents against invasive *Opuntia* species and a fifth one, *Dactylopius coccus,* is reared commercially as a source of the red dye, carmine.

With the increasing importance of commercial cactus plantings and larger areas under cultivation, some of the key pests will find their way to new targets. Knowing and understanding the potential threats may help to prevent unwanted arrivals. The dispersal of *Cactoblastis cactorum* and its subsequent invasion of mainland America is a case study. The chances of insects from non-cactus hosts adapting to become pests on cactus cultivations are small, and the recruitment of new pests in the major cactus growing countries will depend mainly on natural dispersal and human intervention of existing cactus pests. This applies particularly to cactus-pear cultivation in countries outside of the Americas. The recruitment of new pests from the large source of cactus-feeding insects and diseases native to the Americas is also possible in time.

The internal feeding habits of most cactus-feeding insects will make conventional control methods, e.g., insecticidal control, very difficult. Biological control has been attempted against only one cactus pest, *Diaspis echinocacti,* but biological control projects are now being considered against *C. cactorum* and other species. Research will continue on the use of host-specific, cactus-feeding insects for

the biological control of cactus invaders outside their natural distribution. The selection of host-adapted biotypes of *Dactylopius tomentosus* for the biological control of *Opuntia rosea* is presently being examined in South Africa, which is expected to provide further useful information on the existence of host-adapted biotypes. Studies on biological control of cactus weeds have provided valuable information on many of the key cactus-feeding insects (Moran and Zimmermann 1984). Likewise, research on *C. cactorum* by South African and Australian entomologists will provide useful information when formulating a strategy to prevent its invasion or, eventually, its control on the North American continent (Zimmermann et al. 2000).

Cactus diseases are not extensively studied, as revealed by the relatively few publications. Most research on cactus diseases has emerged from Mediterranean countries, e.g., Italy. Even less research has been conducted on the natural diseases found on native cactus species in the Americas. With increased cultivation of cactus pear in America and elsewhere, some of the less host-specific latent diseases are expected to gain in importance when switching to commercial plantations.

Acknowledgments

Thanks are expressed to the following persons for providing information on cactus pests and selected literature: Mayra Perez-Sandi y Cuen, Antonio Bustamante, Yosef Mizrahi, Carmen Saenz, Carlos Nostas, and Enrique Lobo. Hildegard Klein provided valuable criticism and edited the draft manuscript.

Literature Cited

Agrios, G. N. 1978. *Plant Pathology*, 2nd ed. Academic Press, New York.

Alcorn, S. M., R. L. Gilbertson, and M. R. Nelson. 1975. Some diseases of cacti in Arizona. *Progressive Agriculture in Arizona* 17: 3–6.

Alcorn, S. M., and T. V. Orum. 1988. Rejection of the names *Erwinia carnegieana* 1942 and *Pectobacterium carnegana* (Standring 1942) Brenner, Teigerwait, Miklos and Fanning 1973. *International Journal of Systematic Bacteriology* 38: 132–134.

Annecke, D. P., W. A. Burger, and H. Coetzee. 1976. Pest status of *Cactoblastis cactorum* (Berg) (Lepidoptera: Phycitidae) and *Dactylopius opuntiae* (Cockerell) (Coccoidea: Dactylopiidae) in spineless *Opuntia* plantations in South Africa. *Journal of the Entomological Society of Southern Africa* 39: 111–116.

Annecke, D. P., and V. C. Moran. 1978. Critical reviews of biological pest control in South Africa. 2. The prickly pear, *Opuntia ficus-indica* (L) Miller. *Journal of the Entomological Society of Southern Africa* 41: 161–188.

Backeberg, C. 1976. *Das Kakteenlexicon.* Gustav Fischer Verlag, Stuttgart.

Barbera, G. 1995. History, economic and agro-ecological importance. In *Agro-ecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 1–11.

Barthlott, W., and D. R. Hunt 1993. The Cactaceae. In *The Families and Genera of Vascular Plants.* (K. Kubitzki, ed.). Springer-Verlag, Berlin. Pp. 161–197.

Behailu, M., and F. Tegegne (eds.). 1997. *Proceedings of the International Workshop on Opuntia in Ethiopia: State of Knowledge in Opuntia Research.* Mekelle University College, Mekelle, Ethiopia.

Benson, L. 1982. *The Cacti of the United States and Canada.* Stanford University Press, Stanford, California.

Blanchard, E. E. 1922. Apuntes sobre *Zophodia analamprella* Dyar y otros Lepidopteros que viven sobre Cactaceae en la Argentina. *Physis* 6: 119–123.

Bradbury J. F. 1970. Isolation and preliminary study of bacteria from plants. *Reviews of Plant Pathology* 49: 213–218.

Bravo, H. H. 1978. *Las Cactaceas de Mexico.* Universidad Nacional Autónoma de Mexico, Mexico City.

Brutsch, M. O., and H. G. Zimmermann. 1995. Control and utilization of wild opuntias. In *Agro-ecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 155–166.

Buchanan, R. E., and N. E. Gibbons. 1974. *Bergey's Manual of Determinative Bacteriology*, 8th ed. Williams & Wilkins, Baltimore, Maryland.

Cacciola, S. O., and G. Magnano di San Lio. 1988. Foot rot of prickly pear cactus caused by *Phitophthora nicotianae. Plant Disease* 72: 793–796.

Chessin, M. 1965. Wild plant hosts of a cactus virus. *Phytopathology* 55: 933.

Cockerell, T. D. A. 1929. Biological control of prickly-pear. *Science* 69: 328–329.

Cortés, L., and L. Fucikovsky. 1986. Pudrición blanda de las pencas del nopal (*Opuntia* sp.). *Memorias XIII Con-*

gresso Nacional de Fitopatologia. Tuxtla Gutiérrez, Mexico. P. 194.

De Arruda, G. P., F. G. P. Arruda, and J. F. Warumby. 1999. Introducción y utilización de las Cactaceas *Nopalea cochenilifera* (L.) y *Opuntia ficus-indica* en Brasil. *Proceedings of the VIII Congreso Nacional y VI Internacional sobre el Conocimiento y Aprovechamiento de Nopal.* San Luis Potosí, Mexico. Pp. 101–102.

De Lotto, G. 1974. On the status and identity of the cochineal insects (Homoptera: Coccoidea: Dactylopiidae). *Journal of the Entomological Society of Southern Africa* 37: 167–193.

Dodd, A. P. 1940. The biological campaign against prickly-pear. *Commonwealth Prickly Pear Board Bulletin.* Brisbane, Australia. Pp. 1–177.

Eisner, T., S. Nowicki, M. Goetz, and J. Meinwald. 1980. Red cochineal dye (carminic acid): Its role in nature. *Science* 208: 1039–1042.

Farr, D. F., G. F. Bills, G. P. Chamuris, and A. Y Rossman. 1989. *Fungi on Plants and Plant Products in the United States.* APS Press, St. Paul, Minnesota.

Fucikovsky, L. 1990. Associación de insectos con la prudicíon blanda de cladodios. *Resumenes IV Reunion Nacional sobre el Conocimiento y Aprovechamiento del Nopal.* Zacatecas, Mexico. P. 38.

Gallegos Vasquez, C., and S. de J. Mendez Gallegos. 2000. La tuna: criterios y técnicas para su producción comercial. *Fundación Produce Zacatecas.* Universidad Autónoma Chapingo, Chapingo, Mexico. Pp. 95–116.

Githure, C. W., H. G. Zimmermann, and J. H. Hoffmann. 1999. Host specificity of biotypes of *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae): Prospects for biological control of *Opuntia stricta* (Haworth) Haworth (Cactaceae) in Africa. *African Entomology* 7: 43–48.

Granata, G., and L. Varvaro. 1990. Bacterial spots and necrosis caused by yeasts on prickly pear cactus in Sicily. *Proceedings of the 8th Congress of the Mediterranean Phytopathological Union,* Agadir, Morocco. Pp. 467–468.

Gutiérrez, L. H. 1992. *Plagas y Enfermedades del Nopal en México.* Universidad Autónoma Chapingo, Chapingo, Mexico.

Hernandez, J. C. 1992. Plagas, enfermedades y otros factores que afectan al nopal. *Proceedings of the V National and III International Congress on the Understanding and Utilization of Cactus Pear.* Chapingo, Mexico. P. 89.

Hernandez, J. C, L. Fucikovsky, and A. R. Dionicio. 1997. Erwinias en la pudrición del nopal (*Opuntia* spp.) en differentes zonas nopaleras de Mexico. *Proceedings of the VII National and V International Congress on the Understanding and Utilization of Cactus Pear.* Monterrey, Mexico. Pp. 193–194.

Hoffmann, J. H. (ed.). 1991. Biological control of weeds in South Africa. *Agriculture, Ecosystems and Environment* 37: 1–255.

Hoffmann, J. H., and H. G. Zimmermann. 1989. Ovipositional and feeding habits in cactophagous pyralids: Prediction for biological control of cactus weeds. *Proceedings of the VII Symposium on Biological Control of Weeds.* MAF, Rome. Pp. 395–399.

Hosking, R. J. 1984. The effect of temperature on the population growth potential of *Dactylopius austrinus* De Lotto (Homoptera: Dactylopiidae) on *Opuntia aurantiaca. Journal of the Australian Entomological Society* 23: 133–159.

Hunter, W. D., F. C. Pratt, and J. D. Mitchell. 1912. The principal cactus insects of the United States. *United States Department of Agriculture, Entomological Bulletin* 113: 1–71.

Karny, M. 1972. Comparitive studies on three *Dactylopius* species (Homoptera: Dactylopiidae) attacking introduced opuntias in South Africa. *Department of Agricultural Technical Services, Entomology Memoir* 26: 1–19.

Kreger, N., and W. R. van Rij. 1984. *The Yeasts. A Taxonomic Study,* 3rd ed. Elsevier, Amsterdam.

Krieg, N. E. 1984. *Bergey's Manual of Systematic Bacteriology,* 8th ed., Vol. 1. Williams & Wilkins, Baltimore, Maryland.

Johnson, D. M., and P. D. Stiling. 1998. Distribution and dispersal of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an exotic *Opuntia*-feeding moth, in Florida. *Florida Entomologist* 81: 12–22.

Julien, M. H., and M. W. Griffiths (eds.). 1998. *Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds,* 4th ed. CABI Publishing, Wallingford, United Kingdom.

Lawton, J. H., and D. Schröder. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with plants. *Nature* 265: 137–140.

Lelliot, R. A., and D. E. Stead, 1987. *Methods for the Diagnosis of Bacterial Diseases of Plants.* Blackwell, Oxford.

Lodder, J. (ed.). 1974. *The Yeasts: A Taxonomic Study.* North-Holland, Amsterdam.

Longo, S., and C. Rapisarda. 1995. Pests of cactus pear. In *Agro-ecology, Cultivation and Uses of Cactus Pear.* FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 100–108.

Magnano di San Lio, G., and A. Tirrò. 1973. Una moria del ficodindia causata da *Armillaria mellea. Informatore Fitopatologico* 1: 47–50.

Mann, J. 1969 *Cactus-Feeding Insects and Mites.* Smithsonian Institution Bulletin 256, Washington, D.C.

McFadyen, R. E. 1985. Larval characteristics of *Cactoblastis* spp. (Lepidoptera: Pyralidae) and the selection of species for biological control of prickly pears (*Opuntia* spp.). *Bulletin of Entomological Research* 75: 159–168.

Mildenhall, J. P., S. M. Alcorn, and W. F. O. Marasas. 1987. Pathogenecity of fungi isolates from *Opuntia* species in Arizona to *Opuntia aurantiaca. Phytophylactica* 19: 485–489.

Mitchell, J. K. 1985. Disorders of natural and commercially grown cacti: A literature review. *Cactus and Succulent Journal (U.S.)* 57: 226–231.

Mizrahi, Y., and A. Nerd. 1999. Usage of various cactus species as fruit and vegetable crops in Israel. *Proceedings of the VII National and VI International Congress on the Understanding and Utilization of Cactus Pear.* San Luis Potosí, Mexico. Pp. 240–254.

Moran, V. C. 1980. Interactions between phytophagous insects and their *Opuntia* hosts. *Ecological Entomology* 5: 153–164.

Moran, V. C. 1983. The phytophagous insects and mites of cultivated plants in South Africa: Patterns and pest status. *Journal of Applied Ecology* 20: 239–250.

Moran, V. C., and D. P. Annecke. 1979. Critical reviews of biological pest control in South Africa. 3. The jointed cactus, *Opuntia aurantiaca* Lindley. *Journal of the Entomological Society of Southern Africa* 42: 299–329.

Moran, V. C., and B. S. Cobby. 1979. On the life history and fecundity of the cochineal insect, *Dactylopius austrinus* De Lotto (Homoptera: Dactylopiidae), a biological control agent for the cactus *Opuntia aurantiaca. Bulletin of Entomological Research* 69: 629–636.

Moran, V. C., and J. H. Hoffmann. 1987. The effects of simulated and natural rainfall on cochineal insects (Homoptera: Dactylopiidae): Colony distribution and survival on cactus cladodes. *Ecological Entomology* 12: 61–68.

Moran, V. C., B. H. Gunn, and G. H. Walter. 1982. Wind dispersal and settling of first-instar crawlers of the cochineal insect *Dactylopius austrinus* (Homoptera: Coccoidea: Dactylopiidae). *Ecological Entomology* 7: 409–419.

Moran, V. C., and H. G. Zimmermann. 1984. The biological control of cactus weeds: Achievements and prospects. *Biocontrol News and Information* 5: 297–320.

Morrison, J. F. 1984. Protection from beetle-predation in cochineal insects (Dactylopiidae: Homoptera). Master's Thesis, Rhodes University, Grahamstown, South Africa.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Ochoa de Cornelli, M. J., G. Ayrault, C. Degano, and M. S. Lopez Alsogaray. 1992. El cultivo de la tuna (*Opuntia ficus-indica)* en la Provincia de Santiago del Estero, Argentina. *Actas de II Congreso Internacional de Tuna y Cochinilla.* Santiago, Chile. Pp. 97–102.

Olckers, T., and M. P. Hill (eds.). 1999. Biological control of weeds in South Africa (1990–1998). *African Entomology Memoir* 1: 1–182.

Ortega, J. A. 1991. *Alejandro de Humboldt: Ensayo Politico sobre el Reino de la Nueva España.* Editorial Porrua, Mexico City.

Pemberton, R. W. 1995. *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in the United States. An immigrant biological control agent or an introduction of the nursery industry? *American Entomologist* 41: 230–323.

Perez Guerra, G., and M. Kosztarab. 1992. Biosystematics of the family Dactylopiidae (Homoptera: Coccinea) with emphasis on the life cycle of *Dactylopius coccus* Costa. *Virginia Agricultural Experimental Station, Bulletin* 92–1. Virginia Polytechnic Institute and State University, Blacksburg. Pp. 1–87.

Pettey, F. W. 1948. The biological control of prickly-pear in South Africa. *Science Bulletin, Department of Agriculture of the Union of South Africa* 271: 1–163.

Phaff, H. L., W. T. Starmer, M. Miranda, and M. W. Millen. 1978. *Pichia heedii,* a new species of yeasts indigenous to necrotic cacti in the North American Sonoran Desert. *International Journal of Systematic Bacteriology* 28: 326–331.

Phaff, H. L., W. T. Starmer, J. Tredick, and M. Miranda. 1985. *Pichia deserticola* and *Candida deserticola,* two new species of yeasts associated with necrotic stems of cacti. *International Journal of Systematic Bacteriology* 35: 211–216.

Pimienta-Barrios, E. 1974. Estudio de las causas que pro-

ducen el engrosamiento de cladodios en nopal (*Opuntia* spp.) en la zona de Chapingo. Master's Thesis, Colegio de Postgraduados, Chapingo, Mexico.

Raabe, R. D. 1979. Some previously unreported hosts of *Armillaria mellea* in California III. *Plant Disease Reporter* 63: 494–495.

Redfern, D. B. 1968. The growth rate of *Armillaria mellea. Transactions of the British Mycological Society* 51: 575–586.

Redfern, D. B. 1973. Growth and behaviour of *Armillaria mellea* rhizomorphs in soil. *Transactions of the British Mycological Society* 61: 568–581.

Robertson, H. G. 1987. Oviposition site selection in *Cactoblastis cactorum* (Lepidoptera): Constraints and compromises. *Oecologia* 73: 601–608.

Robertson, H. G., and J. H. Hoffmann. 1989. Mortality and life-tables on *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) compared on two host-plant species. *Bulletin of Entomological Research* 79: 7–17.

Robles, M. A. J. 1999. Respuesta de la grana de cochinilla en diferentes cultivares de nopal. *Proceedings of the VIII Congreso Nacional y VI Internacional Sobre el Conocimiento y Aprovechamiento del Nopal.* San Luis Potosí, Mexico. Pp. 113–114.

Scheinvar, L. 1999. Biosistematica de los xoconostles mexicanos y su potencial económico. *Proceedings of the VIII National Congress and IV International Congress on the Understanding and Utilization of Cactus Pear*. San Luis Potosí, Mexico. Pp. 255–274.

Skerman, V. B. D., V. Mc Gowan, and P. H. A. Sneath. 1980. Approved lists of bacterial names. *International Journal of Systematic Biology* 30: 225–420.

Stange, G., J. Monro, S. Stowe, and C. B. Osmond. 1995. The CO_2 sense of the moth *Cactoblastis cactorum* and its probable role in the biological control of the CAM plant *Opuntia stricta. Oecologia* 102: 341–352.

Starmer, W. T., H. S. Phaff, M. Miranda, and M. W. Miller. 1978. *Pichia captophila,* a new species of yeast found in decaying tissue of cacti. *International Journal of Systematic Bacteriology* 28: 318–325.

Strong, D. R. 1979. Biogeographic dynamics of insect-host plant communities. *Annual Review of Entomology* 24: 89–119.

Strong, D. R., and D. A. Levin. 1979. Species richness of plant parasites and growth form of their hosts. *American Naturalist* 114: 1–22.

Tito, S. M. 1998. Plagas y enfermedades del nopal que afectan la producción de grana-cochinilla *Dactylopius coccus* Costa. *Memorias del Primer Congreso Internacional de Grana Cochinilla y Colorantes Naturales.* Oaxaca, Mexico. Pp. 39–40.

Varvaro, L., G. Granata, and G. M. Balestra. 1993. Severe *Erwinia* caused damage on *Opuntia ficus-indica* in Italy. *Journal of Phytopathology* 138: 325–330.

Volchansky, C. R., J. H. Hoffmann, and H. G. Zimmermann. 1999. Host-plant affinities of two biotypes of *Dactylopius opuntiae* (Homoptera: Dactylopiidae): Enhanced prospects for biological control of *Opuntia stricta* (Cactaceae) in South Africa. *Journal of Applied Ecology* 36: 85–91.

Von Arx, J. A. 1984. Notes on *Monographella* and *Microdochium. Transactions of the British Mycological Society* 82: 373–374.

Went, F. W. 1982. The physiology of Cacti. In *The Cacti of the United States and Canada* (L. Benson, ed.). Stanford University Press, Stanford, California. Pp. 56–62.

Witbooi, W. R. 1991. Evaluation of *Opuntia* pathogens obtained from Arizona cacti to *Opuntia aurantiaca.* Master's Thesis, University of Fort Hare, Alica, South Africa.

Wollenweber, H. W., and O. A. Reinking. 1935. *Die Fusarien. Ihre Beschreibung, Schadwirkung und Bekämpfung*. Verlag Paul Parey, Berlin.

Wright, E. R. 1997. Identificación del patógeno productor de una mancha en cladodios de *Opuntia ficus-indica.* Bachelor's Thesis, Universidad de Buenos Aires, Buenos Aires, Argentina.

Zimmermann, H. G., and V. C. Moran. 1982. The ecology and management of cactus weeds in South Africa. *South African Journal of Science* 78: 314–320.

Zimmermann, H. G., R. E. McFadyen, and H. E. Erb. 1979. Annotated list of some cactus-feeding insects of South America. *Acta Zoologica Lilloana* 32: 101–112.

Zimmermann, H. G., and M. Perez-Sandi y Cuen. 1999. A new insect pest on Opuntiae in wait for Mexico. *Proceedings of the VIII National Congress and the VI International Congress on the Understanding and Utilization of Cactus Pear.* San Luis Potosí, Mexico. Pp. 333–341.

Zimmermann, H. G., V. C. Moran, and J. H. Hoffmann. 2000. The renowned cactus moth, *Cactoblastis cactorium:* Its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. *Diversity and Distributions* 6: 259–269.

CHAPTER

› 15 ‹

BREEDING AND BIOTECHNOLOGY

Brad Chapman, Candelario Mondragon Jacobo, Ronald A. Bunch, and Andrew H. Paterson

Introduction
- *Breeding and Biotechnology Research Objectives*
- *Expanding Markets*

Breeding
- *Breeding programs*
- *Germplasm Pools*
- *The Cultivated Gene Pool*
- *The Semidomesticated and Wild Gene Pool*
- *Germplasm Collections*
- *Breeding Systems and Techniques*
- *Controlled Pollination*
- *Clonal Propagation/Apomixis*
- *Future Directions*

Biotechnology
- *Overview of Plant Molecular Tools*
- *DNA and Protein Analysis*
- *Tissue Culture and Transformation*
- *Evolutionary Relationships*
- *Molecular Tools for Cacti*
- *Future Directions*

Conclusions

Literature Cited

Introduction

This chapter focuses on the highly important fruit-bearing group of the genus *Opuntia,* although the techniques, methods, and concepts presented are transferable to most of the Cactaceae. Because cactus germplasm can be improved via plant breeding and molecular techniques, genetic resources and current objectives for breeding and biotechnology are discussed. A summary of molecular genetic research involving cactus is followed by a plan for utilizing the work from other plant species to advance the biotechnology of cactus.

The previous chapters leave little doubt about the uniqueness and usefulness of the Cactaceae; unfortunately, the family has been underutilized as a target for improvement using plant breeding and biotechnological

techniques. The multiple uses and the ability of cacti to thrive in arid and semiarid environments that many other species are unable to tolerate make it of immediate interest to breeders and molecular biologists seeking to develop crops for areas typically unsuitable for conventional agriculture. The most obvious trait of interest is the ability of cacti to be productive under water-limited conditions (Nobel 1988). Coupled to the drought-tolerant phenotype is the ability of cacti to tolerate high growth temperatures. Third, another well-studied feature of cacti is their ability to thrive under elevated atmospheric carbon dioxide levels (Nobel 1991a; Cui et al. 1993; Nobel and Israel 1994). In addition, cacti have an extremely high productivity under optimal conditions (Nobel 1991b). Cacti are economically important and physiologically interesting, making them a worthy and intriguing subject for breeding and molecular work. Because the cacti used today are primarily wild plants that have merely been domesticated, advances in plant breeding and biotechnology could extend the growing range into new environments and could generate new uses for cactus products. Defining objectives for these investigations will be an essential part of developing organized and productive breeding and molecular biological programs.

Breeding and Biotechnology Research Objectives

The broad goals of both biotechnology and breeding research for cacti are to understand the molecular mechanisms underlying interesting and useful traits and to use this understanding to develop crops that are better suited to human needs. Improvement must be intimately tied to the needs of growers, processors, and consumers. Because cacti lack the extensive breeding history of other crops, many avenues of research on the improvement of cactus germplasm are possible. The priority of research goals will vary depending on the production region and the local uses of cacti. Improvements to cactus varieties will fall into three main categories: (1) expanding the production area into new environments, (2) improving the quality and productivity of cacti to expand into new markets, and (3) adding new traits to allow the development of new uses for cacti.

Cacti are well adapted to the arid and semiarid regions where food and fodder crops are limited, although minimum temperatures substantially limit the growing range in some areas (Wang et al. 1997). Thus, a primary biotechnological goal should be to expand the production area for cacti by producing cold-tolerant cultivars. Current high-yielding fruit, vegetable, and forage varieties are killed by temperatures of −5 to −8°C (Loik and Nobel 1991; Parish and Felker 1995; Wang et al. 1997). Nevertheless, wild opuntias have a broad geographic range, including southern Canada (Loik and Nobel 1993). Vast areas of the south-central United States and northern Mexico would be available to grow cacti if cold tolerance could be introduced to highly productive, high-quality varieties. Because researchers are beginning to elucidate the mechanisms for cold tolerance in *Opuntia* germplasm, the immediate objective should be to understand the genetic basis for this tolerance and begin to integrate this into commercially useful varieties with a minimal transfer of undesired characteristics. For fruit production, chilling requirements may be an important aspect for research. For instance, exposure to day/night temperatures of 15/5°C versus 35/25°C produces significantly more floral than vegetative buds for *Opuntia ficus-indica* (Nobel and Castañeda 1998). Genetic manipulation of the chilling requirements of temperate fruit crops is common. Employing similar techniques for *Opuntia* species will help expand fruit production areas to the tropics and subtropics. In addition, out-of-season production would be possible in established cactus production areas.

Increased disease and insect resistance is probably a prerequisite for introducing cactus varieties into new regions. In general, cacti are relatively tolerant of diseases and insects (Chapter 14), although several diseases attack them (Granata and Sidoti 1997; Saad et al. 1998), and more cactus diseases are likely to appear as cactus production spreads. Cultivars with both broad-based resistance and disease specific resistance will be essential for maintaining consistently high yields.

Various biological questions relating specifically to cacti potentially have long-term applied value. Understanding the molecular basis of adaptations conferring drought and high-temperature tolerance has implications for increasing drought and temperature tolerance in other crop species and is of general interest for understanding plant physiology. Similarly, cacti may prove to be important organisms to study the molecular genetics and evolutionary conservation of CAM (Cushman and Bohnert 1997). A greater understanding of cactus polyploidy will be useful for both basic and applied research. The basal number of chromosomes is $n = 11$ (Pinkava et al. 1985, 1992). Many wild species are diploids, although polyploids up to $2n = 19x = 209$ or higher occur (Mondragon 1999). The amazing range of chromosome numbers for cacti presents an opportunity to study the basis of polyploidy that is paralleled among cultivated plants only by sugarcane. In ad-

dition, understanding the mechanisms behind this polyploid nature may help facilitate crosses between cacti of different ploidy levels, reducing some of the genetic barriers for hybridization. Immense opportunities exist for breeding and biotechnological studies of cacti. This chapter outlines specific research that can accomplish objectives and answer questions discussed above. Areas are emphasized where different disciplines can make important contributions.

Expanding Markets

Although cactus pears are a coveted fruit by many and a staple seasonal fruit in some areas of the world, their consumption is generally limited to ethnic groups with a historical association with the fruit. Seeds, which are typically swallowed along with the pulp, are the major deterrent to attracting new consumers to cactus pear. The seed count ranges from 80 to more than 300 per fruit (Pimienta 1990; Barbera et al. 1991), which means there are 3 to 8 grams of seeds per fruit, depending on fruit size and the cultivar (Mondragon and Perez 1996). Unbalanced gametes as a result of polyploidy can lead to the partial seed set commonly observed for *O. ficus-indica* (Nerd and Mizrahi 1994). The ratio between aborted and normal seeds is higher in Italian (0.44) than in Mexican cultivars (0.11; Pimienta and Mauricio 1987; Barbera et al. 1994). Seed content is positively correlated with fruit size, and large fruits command a premium price in the market. Thus the ideal fruit should have a large number of seeds to attain good size, but a high ratio of aborted to normal seeds.

The environmental and crop management factors influencing seed content have not yet been separated from genetic factors. Parthenocarpy (production of fruits without seeds because of lack of pollination or fertilization, or fertilization followed by embryo abortion) has also been mentioned as a solution to the problem of seediness in the fruit. Natural parthenocarpy was reported in BS1, a yellow fleshed accession studied in Israel that does not require pollination for fruit set and development (Weiss et al. 1993; Nerd and Mizrahi 1994). However, the degenerated seeds still contain hard arils, and the overall fruit quality is low. Several attempts have been made to reduce the size of the seeds by means of gibberellin application but with little success (Gil and Espinosa 1980; Aguilar 1987; Ortiz 1988).

Fruit size and shape as well as pulp color are important factors to consider when developing new cultivars of cactus pear. Large fruits are preferred. Also, oval or barrel-shaped fruits are easier to harvest than elongated fruits and therefore suffer less harvest damage to the stem end (Cantwell 1991). In Mexico, green-white pulp is preferred, in Italy and northern Europe yellow-orange pulp is preferred, and in the United States and Canada red pulp is often favored. Pulp juiciness and the high content of soluble solids are considered important fruit quality factors (Wang et al. 1998). For some markets, fruits with higher acid content are favored (Saenz and Costell 1990). Postharvest handling, packing, and storage need to be considered when developing new cultivars of cactus pear for commercial use (Corrales-Garcia et al. 1997).

Although spine density and size on the cladodes vary among accessions (collected wild varieties or cultivars), some spines are present even in so-called spineless cultivars. Spineless individuals do not occur in the wild, indicating that this trait was acquired through domestication. In regard to crop management, spines represent an inconvenience because they hamper routine operations, such as pruning, and represent an important obstacle at harvest time. Commercial varieties for fruit in Mexico are spiny (with the exception of 'Roja Lisa'). Other producing countries rely on spineless cultivars, and efforts to develop new varieties should be focused on producing spineless types.

The presence of glochids on the fruit peel is also a major constraint to increased consumption. Selection and breeding for glochid-free varieties should be a priority (Barbera 1995). Another solution is to develop cultivars with easily shed glochids. Genes for low numbers of areoles and short glochids are present in *O. robusta,* although the fruit of this species is not well accepted due to its low sugar content, bland flavor, and short shelf life.

For cactus used as a vegetable, the presence of spines and glochids is one of the main constraints for the development of a wider market outside Mexico. A solution to this problem is the development of spineless varieties. Another possibility is to implement early screening for low number of glochids on the cladodes as well as short, soft glochids. Moreover, cultivars of *Nopalea* species produce cladodes that are nearly free of spines and glochids, which can help introduce cacti as a vegetable into new markets. The ability to shed the spines and glochids before the cladodes age could be a selection criteria when breeding for new vegetable varieties. Another useful selection criteria could be the shape of the podarius (tubercle); large podaria can facilitate mechanical peeling. Suitability of new accessions to be consumed as a vegetable can be evaluated in the second year, because there is no need to wait until the reproductive stage is reached. Spines, if not properly removed, can also be a problem for feeding livestock. Breeding for increased nutritional content would be a wor-

thy goal to increase the availability of feed in arid and semi-arid regions (Felker 1995a).

Breeding

Cactus pear was domesticated in the highlands of Central Mexico. Reports of consumption of cacti date back to the ancient groups that inhabited Mesoamerica, and evidence exists that agaves and cacti have been part of the human diet for over 9,000 years (Nobel 1994). The transition to planned cultivation of *Opuntia,* a crucial step in the early domestication of wild plants, may have taken place before 8,000 years B.P. (Hoffman 1995). While some traditionally used species (e.g., *Steneocereus* spp., *Hylocereus* spp., and *Selenicereus megalanthus*) are only now being cultivated, cactus pear has been farmed for thousands of years. It is, together with corn, beans, and agave, among the oldest cultivated plants in Mexico.

Cactus pear developed into a formal crop in the 20th century as it evolved from collections of wild plants to exceptional hand-selected individuals grown in backyards. The transition of the rural population toward an urban semi-industrial society created a consumer base for the initial market of cactus pear in the 1960s. During the 1970s through the 1980s, programs initiated by the Mexican government provided an important boost to the cactus pear industry—increasing the area of commercial orchards and establishing research programs. Selection in the last few centuries has led to a number of outstanding cultivars with exceptional fruit quality and productivity, as well as drought and frost tolerance. The outcome of this long-term activity has resulted in six to eight commercial cultivars as the basic stock for the Mexican and Italian markets, currently the most important producers and consumers worldwide.

Breeding Programs

Hybridization of cactus pears was claimed by Luther Burbank in the early 1900s, leading to the development of the so-called Burbank spineless cactus with an immense potential as cattle forage in desert areas. Several varieties produced from extensive crossing and selection among accessions from Mexico, Africa, Australia, and other countries were developed and aggressively marketed (Dreyer 1985). The lack of records and formal publications gave rise to questions about the sources of plant material and methodologies used for the released cultivars. Nevertheless, Burbank was responsible for the distribution of a tremendous amount of *Opuntia* germplasm throughout the world, such as the cactus pear cultivars found today in South Africa (Wessels 1988).

Modern-day cactus pear breeding in Mexico began in 1964 when the late Facundo Barrientos of the Colegio de Postgraduados, Chapingo, began his program for its genetic improvement. The ambitious program included germplasm collection and utilization, breeding of new cultivars, and development of new uses for cactus pear. He envisioned that the ideal cactus pear cultivar should be multipurpose and widely adapted, and he worked toward high fruit quality, high forage quality, drought and heat resistance, and early maturity. In the early years he introduced selections 'COPENA V1' and 'F1' for vegetable and forage, respectively. He developed a series of high-quality white (or green) pulped selections (the 'COPENA T' series) that had only modest commercial success as they did not present a clear advantage over the native white cultivars. Later, he broadened his efforts to include other colored cactus pears and other species of fruiting cacti. The red pulp cultivar 'Frieda' or 'Torreoja' was his last released cultivar. Prior to his untimely death in 1993, Dr. Barrientos interacted with cactus growers and researchers throughout the world and shared with them germplasm and breeding methodologies. He created a spark that ignited the current interest in new cactus varieties and cactus breeding.

A fresh start at breeding is now underway in the United States, South Africa, Israel, and Mexico. Encouraged by the Food and Agriculture Organization of the United Nations, a renewed interest in the collection of wild and semi-domesticated accessions has developed. In addition, the number of publications with information on crop management practices and new uses of cactus pear are increasing.

Germplasm (gene pool) collection and characterization is the major field of interest in most of the Mexican institutions engaged in cactus pear research, reflecting the fact that Mexico is the main reservoir of variability of edible opuntias. A special concern is the rapid disappearance of valuable plant material from wild stocks in northcentral Mexico resulting from the intensive utilization by the cattle and dairy industry. Backyard orchards have been searched for outstanding individuals to widen the limited array of commercial cultivars for fruit and vegetable production. Three state universities and one technical school support these germplasm collection programs. Formal breeding programs, however, are conducted only by the Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP) and the Colegio de Postgraduados. Their breeding efforts are mostly focused on the development of spineless cultivars for fruit production. Potential expansion into new national and foreign markets emphasizes the development of colored, juicy fruits with low seed

content, early fruiting habit, high soluble solids, and tolerance to indigenous pests and diseases. Vegetable and fodder cultivars are also a priority. The recurrent frosts and droughts observed during the last decade are prompting the search for new cultivars with sustained productivity under such conditions. Programs rely on hybridization and selection as breeding tools. The germplasm base for these projects is totally indigenous, and large populations of hybrids and segregants have been in field trials since 1994.

Two institutions in Mexico are pioneering the application of molecular techniques to cactus pear breeding, the Centro de Investigación y Estudios Avanzados (CINVESTAV) in Guanajuato and the Instituto Tecnológico Agropecuario (ITA 20) in Aguascalientes. Their investigations are directed toward the study of enzymes involved in cell wall softening, with the goal of controlling ripening and thus avoiding temporal saturation of the national market. Other areas of research interest include seed storage proteins (Silos-Espino et al. 1999), cactus transformation, and gene transfer to increase protein content. Beginning in the 1980s, Texas A&M University-Kingsville became involved in agronomic research, extension work, and collection and introduction of cactus pear to the United States. The program aims to develop frost-tolerant cultivars to overcome the common limitation to growing cactus in this region. In 1996 the first round of crosses was initiated, marking the beginning of a long-term breeding program. This institution is also responsible for the popularization of the vegetable cultivar 'Spineless 1308' and various cactus products in Texas.

D'Arrigo Brothers, a produce company based in California, started a private breeding program in 1994 to improve their spineless commercial cultivar 'Andy Boy,' which is similar to the 'Rossa' cultivar grown and marketed in Italy and currently dominates the American out-of-season market. The main objective of this program is the improvement of fruit quality. The program utilizes germplasm obtained from Dr. Barrientos and has recently added a portion of the Texas A&M University-Kingsville collection as breeding material. Seedlings from the first crosses were planted into the field in 1997. Other active programs include one located in Sassari, Italy, that is involved in the improvement of fruit quality using naturalized accessions collected in the semiarid Mediterranean region of Italy. Field trials of crossed and open pollinated seedlings were initiated in 1994. In Argentina, evaluation trials of local and introduced accessions are being conducted. In addition, an ongoing collaborative project with the University of Georgia is developing a molecular marker map from progeny of a cross between two Texas A&M accessions. In South Africa, extensive trials are being conducted to evaluate the best local cultivars. In addition, a study has begun utilizing random amplified polymorphic DNA (RAPD) markers to identify cultivars of plant material being sold to growers in that country. In Israel, evaluation of crosses and selections of fruit-producing *Cereus, Hylocereus,* and *Selenicereus* species is underway as part of a large project to develop new fruit crops for that country.

Germplasm Pools

Each of the major germplasm pools (cultivated, semidomesticated, and wild) exhibits traits of interest for the genetic improvement of cactus pear. A wide range of ploidy levels exists among and within the *Opuntia* species. Pimienta and Muñoz (1995) compiled data from several authors and list reported ploidy levels of 2*x,* 3*x,* 4*x,* 5*x,* 6*x,* 8*x,* 10*x,* 11*x,* 12*x,* 13*x,* 19*x,* and 20*x.* The cultivated types of cactus pear generally have higher chromosome numbers ($2n = 6x = 66$ and $2n = 8x = 88$) than the wild populations (usually $2n = 2x = 22$ and $2n = 4x = 44$). Although large crossing studies have yet to be conducted, barriers to cross compatibility are minimal among the cultivated species. Natural hybrids are common in both cultivated and wild populations of cactus pear (Pimienta and Muñoz 1995). Trujillo (1986) obtained viable seeds from crosses of wild *O. streptacantha* with *O. robusta* and *O. leucotricha* with *O. cochinera.* Wang et al. (1996) successfully crossed *O. lindheimeri* with several cultivated cactus pears. In addition, *O. robusta* and cultivated cactus pear have been crossed.

The Cultivated Gene Pool

Cultivated species of cactus pear include *Opuntia ficus-indica, O. albicarpa, O. streptacantha,* and *O. robusta* plus hybrids between *O. ficus-indica* and the others (Pimienta and Muñoz 1995). For breeding purposes, this germplasm pool is best sorted out by cultivar or specific traits of interest rather than by taxonomic species. Modern cultivars of cactus pear are the products of long-term informal, but effective, selection by growers. The most important selection criteria have been fruit size and quality, plant productivity, and tolerance to drought and frosts. The number of cultivars in each of the countries that grow cactus pear varies according to the intensity of usage and the size of the initial germplasm base, with Mexico accounting for the largest diversity.

Three main groups of cactus pear can be recognized according to the color of the peel and pulp: white (or light green), yellow (including deep orange), and red (from light red to deep purple). The most popular white cultivars in Mexico are 'Reyna,' 'Cristalina,' 'Esmeralda,' and 'Bur-

rona.' 'Reyna' sets the standard of quality and dominates the national market (Mondragon and Perez 1993). The national demand in Mexico is supplemented by the orange-pulped 'Naranjona' and 'Amarilla Montesa' and the red-purple 'Roja Lisa' (Mondragon and Perez 1993, 1996; Pimienta and Muñoz 1995). In the United States, the red-fruited cultivar 'Andy Boy' is available from September until April; it is produced only in California where irrigation and mild winters facilitate out-of-season production. In Chile, a cultivar of *O. ficus-indica* known as 'Verde' (Green; Sudzuki 1995) or 'Blanca' (White; Pimienta and Muñoz 1995) is the most common; since 1982, exports to the U.S. market take advantage of the summer harvest season in the Southern Hemisphere, which coincides with winter in the Northern Hemisphere. The cultivars available in the Sicilian area of Italy are 'Gialla' (Yellow), 'Bianca' (White), and 'Rossa' (Red), with 'Gialla' being the most common (Barbera et al. 1992). A 'seedless' cultivar is also known but its commercial cultivation has never been attempted because of the poor quality of the fruits. Production in Israel is based mostly on the cultivar 'Ofer,' which has yellow pulp. In South Africa the varieties available, 40% of which have light-green fruit, originated from 21 spineless types imported from the Burbank Nursery of California in 1914. Besides color, varieties also differ in other pulp characteristics, peel features, post-harvest physiology, and response to environmental factors.

Because the vegetable nopalitos are most widely consumed in Mexico, Mexico is the main source of germplasm. The Universidad Autónoma de Chapingo near Mexico City has assembled an extensive collection; 'Milpa Alta' (*O. ficus-indica*) is the most important cultivar and is cultivated mostly in the region of the same name near Mexico City. 'COPENA V1' is perhaps the second most important vegetable cultivar. Another variety, 'COPENA F1,' was selected for fodder production by Dr. Barrientos in the 1960s, but its tender pads are also suited to consumption as a vegetable. Both have intense green color, a thin epidermis, good flavor, and low acidity (Flores 1995). 'Moradilla,' 'Atlixco,' 'Polotitlan,' and 'Redonda' are further examples of locally selected varieties of *O. ficus-indica* used for vegetable production. In the southwestern states of Michoacan and Jalisco, the 'Nopal blanco' or white cactus pear is the cultivar of choice for nopalitos and tolerates humid conditions (up to 1,600 mm of rainfall annually). The cultivar 'Valtierrilla' is used as a vegetable in central Guanajuato if picked very young. The cultivar 'Spineless 1308' (*O. cochellinifera* or *Nopalea cochellinifera*), selected by Peter Felker from accessions collected in a humid tropical region of Tamaulipas, Mexico, is suitable for field cultivation in the coastal rain-fed areas of Texas and for greenhouse cultivation in frost-prone areas near San Antonio.

The Semi-Domesticated and Wild Gene Pool

A remarkable diversity of locally known semi-domesticated types exist in the native areas of cactus pear, some serving two or even three purposes: fruits, tender pads, and fodder. Traditionally cactus pear plantings are found on small family properties in dry regions. *Opuntia* hedges are concentrated near farmsteads, where they also protect fruit and vegetable gardens. Taxonomically these cactus pear plants are similar to various hybrids in the cultivated germplasm and represent the transition from wild plants to modern commercial cultivars. Their genetic variability is important as a source for new and valuable traits that may be necessary as breeding programs proceed (Hoffman 1995). Outstanding accessions in family orchards provide a source of individuals derived by chance from free natural outcrossings, whose germplasm has only been minimally collected and characterized.

The last reservoir of interesting individuals is wild populations. Several efforts have been made to collect representatives from the wild populations of fruit-producing *Opuntia* species in Mexico. In 1993, Mexico, Israel, and the United States joined efforts to collect in the highlands of northern Mexico and assembled 130 accessions of fruit-producing *Opuntia* species, selected primarily for cold hardiness (Felker 1995b). Similar endeavors have collected several accessions of the hardy Texas native *Opuntia lindheimeri.* Crosses among many of these species have been successful (Wang et al. 1996), although little information is available for crosses outside of this limited germplasm.

Germplasm Collections

Germplasm collections of cactus pear are maintained at several locations around the world (Table 15.1). The largest number of collections and of entries are located in Mexico, where the greatest diversity occurs for native cactus pear. In addition, each breeding project and cactus pear research program has a collection of at least some of this material (often combined with local accessions).

Due to the genetic makeup of cactus pear, its long-lived perennial habit, and large plant size, the maintenance of germplasm banks is difficult and costly. Collecting plant material based on morphological traits and common local names often leads to duplicated accessions within a collection. The morphology of *Opuntia* species is greatly influenced by the environment; their rapid growth means their reactions to environmental changes are also fairly rapid and more drastic than other cacti. For instance, traits

TABLE 15.1

Major cactus pear germplasm collections

Institution	Collection locations	Approximate number of entries and description	Contacts
		Mexico	
Instituto Nacíonal de Investígaciones Forestales, Agrícolas y Pecuarías (INIFAP)	Palma de la Cruz, San Luis Potosi; San Luis de la Paz, Guanajuato; Sandovales, Aguascalientes; Tecamachalco, Puebla; Ensenada, Baja California Norte	800 entries, mostly from central Mexico, commercial cultivars, and backyards; 95% fruit types, 5% vegetable	Dr. Candelario Mondragon J. or M. C. Rafael Fernández M.
Universidad Autonoma de Chapingo	Chapingo, México; El Orito, Zacatecas	160 entries with a wide variety of cultivars from all over Mexico; mostly for fruit, ~24 for vegetable, and some for fodder	Ing. Claudio Flores Valdez and Dr. Clemente Gallegos F.
Secretaria de Educacion Publica (SEP)	Villa Hidalgo, Zacatecas	90 entries of various Mexican cultivars	Ing. Eloy Rodríguez
Universidad Autonoma de Nuevo Leon	Marin, Nuevo León	110 entries; many for vegetable	Dr. Rigoberto Vázquez A.
		United States	
Texas A&M University, Kingsville	Kingsville, Texas	180 entries of cultivated and wild plants from northern Mexico, southwestern United States, and a few other countries; mostly fruit, some for vegetable and forage, including cold hardy types	Dr. Robert Morgan
		South Africa	
Department of Agriculture, Land and Environment	Pietersburg, Northern Province	80 entries of South African cultivars, selections, and chance hybrids from Burbank material	Mr. Johan Potgieter
		Italy	
University of Palermo	Palermo	45 entries from Italy, South Africa, Chile, and Argentina; fruit	Dr. Paolo Inglese
Dipartimento di Colture Arboree di Università di Sassari	Sassari	Fruit	Dr. Innocenza Chessa

such as spininess, cladode shape and size, fruit characteristics, and plant productivity are affected by the environment (Weniger 1984). Duplication within collections is very common and complicates the evaluation and utilization of the genetic resources. A major cause of the duplication among collections is that each research group may maintain separate stocks to have access to as much genetic variability as possible. Increased characterization of these collections is vitally important to the success of cultivar improvement in cactus pear; however, data collection and analysis for these collections will be quite expensive. Only limited exchange of cactus germplasm has taken place since 1992, when the international cooperation regarding cactus pear formally began. More flexible exchange of germplasm among countries is restricted due partly to the lack of accessible data from the collections and partly to regulations. Despite these limitations, basic descriptions are available for the most important cultivars and outstanding accessions from Mexico (Pimienta and Muñoz 1995; Mondragon and Bordelon 1996), Italy, South Africa, Argentina, and Chile (Pimienta and Muñoz 1995).

An important component of developing successful cactus breeding programs will be utilizing the diversity available. Thus methods for classification of this diversity will need to be developed concurrently with cactus breeding programs (Mondragon 1999). Principal Component Analysis is a powerful multivariate statistical technique to group and visualize the relationship among cultivars based on a number of morphological measurements (Hillig and Iezzoni 1988). Such analysis of 32 cactus pear accessions from central Mexico based on 17 measured traits (Mondragon 1999) indicates a positive relationship between cladode width and fruit weight. This can be used in breeding programs to select for fruit size in juvenile plants, instead of waiting until a plant reaches maturity. A positive correlation also exists between the number of areoles on the cladodes and the number of areoles on the fruit (Mondragon 1999). Three groups incorporating eight of the measured traits are the most important in describing the cultivars: plant vigor, frequency of areoles, and spininess, which together encompass 71% of the variability among the plants. The 32 accessions fall into seven categories: wild accessions, small-fruited plants, "spineless," improved varieties, varieties cultivated for fruit production, very spiny accessions, and a single cultivar 'Cristalina,' that showed extremely vigorous growth. This approach for characterizing accessions will facilitate the incorporation of available germplasm into breeding programs by allowing researchers to narrow their focus to single accessions within each major category.

Breeding Systems and Techniques

Cactus flowers are typically relatively large and hermaphroditic with abundant stamens, a single style, and showy perianth parts (Nerd and Mizrahi 1997). The structure of these flowers suggests that they are cross pollinating and, in fact, insect pollination is quite common. For cactus pear under natural conditions, pollination by insects (mainly bees) ensures a high number of seeds once the flower opens. In the fruit-producing *Opuntia* species, self-compatibility and self-pollination occur, and bagged flowers can set fruit (Nerd and Mizrahi 1997). Protandry can explain self-pollination prior to flower opening. Little information is available regarding the ability of wild cactus species to self-pollinate. Bagged flowers of *O. lindheimeri* did not produce fruits in one study (Grant et al. 1979). However, five out of ten bagged flowers of *O. lindheimeri* set fruit and produced seed in another study (Wang et al. 1996). With regard to other species of fruiting cacti, clones of *Cereus peruvianus, Hylocereus costaricensis ,* and *H. polyrhizus* are self-incompatible and those of *H. undatus* and *Selenicereus megalanthus* are self-compatible. Sicilian cultivars of cactus pear are self-compatible, as problems of fruit set are seldom encountered in vegetatively propagated plantations composed of a single cultivar or in single plants grown in backyards (Nerd and Mizrahi 1997). Similarly in the Pyramids region of central Mexico, about 7,000 ha of the cultivar 'Reyna' are cultivated without apparent pollination problems.

Controlled Pollination

Short-term pollen storage for less than a week can be accomplished by collecting buds close to flowering and placing them in a cool and shaded location. Before use, the buds are exposed to full sun for a few hours to promote flowering. Unopened buds can also be used, but their pollen yield is lower. Pollen collected fresh or stored at room temperature for up to 6 days will remain viable and effect successful pollination (Bunch 1997). To facilitate germination, five milligrams of cactus pollen are suspended in 5 ml of germination medium prepared with 100 ppm H_3BO_4, 300 ppm $Ca(NO_3)_2 \cdot 4H_2O$, 200 ppm $MgSO_4$, and 100 ppm KNO_3 in a 40% sucrose solution.

The emasculation (removal of the stamens) of a cactus pear flower resembles a surgical operation and as such should be performed carefully (Fig. 15.1). The material needed includes rubber gloves, a brush, a sharp knife or razor blade, small scissors with a bent tip, a rinsing bottle, paper towels, glassine or paper bags, and rubber bands. When emasculating flowers of cactus pear, take the fol-



Figure 15.1. Methodology for emasculating flowers of cactus pear: (A) emasculating an *Opuntia ficus-indica* flower; (B) washing the emasculated flower; (C) covering the emasculated flower with a bag; and (D) pollinating the emasculated flower with an open flower.

lowing steps: (1) clean the exterior of the buds with the brush to allow easy handling; (2) excise the corolla, using as few strokes as possible, avoiding wounds and mechanical damage to the style; (3) carefully remove the stamens and anthers, cutting close to the base; (4) rinse thoroughly with clean water to get rid of pollen residues and anthers; and (5) cover the emasculated flower bud with a bag to prevent unwanted pollination.

Although it is important to minimize damage to the flower during emasculation, the flowers are able to recover from some damage to the receptacle without significantly harming reproductive potential. The wound response of cactus involves the abundant flow of mucilage from the wounds. This mucilage covers the wound and dries, thereby reducing water loss and preventing infections. It is important that the stigma and style remain intact and undamaged. Even young flowers can be emasculated without appreciable loss of fertility. However, handling very young buds is difficult, because the stamens tend to be less exposed and the risk of mechanical damage to the stigma and style is greater. The application of Dithyocarbamate (Sevin, 2%) powder in the receptacular cavity after partial emasculation can prevent insect visitation and undesired pollination (Wang et al. 1996).

After emasculation, the stigma becomes receptive in 3 to 4 days; however, under warm (> 35°C) conditions, it is receptive earlier. When the stigma is receptive, it is shiny and sticky and the lobes are wide open. The most efficient way to pollinate is using a detached, fresh, fully open flower devoid of its style and corolla to allow close rubbing of the stamens with the stigma of the female flower. Stored pollen can be applied onto the stigma of an emasculated flower with a #3 camelhair paintbrush (Bunch 1997). Partially opened buds can also be used, taking advantage of the protandric nature of cactus pear pollination. Longer availability of flowers for crossings can be accomplished by eliminating the first flowering flush, which ensures that after 50 to 70 days a new round of crosses can be per-

formed. In general, crosses performed later in the flowering season reduce the number of normal seeds. Typically 100 to 250 normal seeds can be obtained from a single fruit, depending upon the crossing conditions and the cultivars involved in the cross. The difficulty involved in emasculation and the high number of seeds that can be expected from a single fruit underscores the importance of having a few carefully performed crosses rather than numerous potentially unsuccessful ones.

Self-pollination can easily be performed by bagging unopened cactus flowers to avoid cross pollination. Moving pollen from the anthers to the stigma of the same flower often results in increased seed set. Typically, inbreeding of a cross-pollinated and vegetatively propagated crop does not result in superior progeny, although this has not been confirmed for cacti. In addition, self-pollinated progeny will help elucidate genetic factors controlling important traits by unlocking genes hidden behind heterozygosity in these out-crossing species. Trials are currently underway to document differences among various breeding methods.

Seeds should be extracted from ripe and healthy fruits. Fruits are peeled and processed in a blender at low speed. Seed disinfection is accomplished by soaking the seeds in commercial bleach (5–6% sodium hypochlorite) for 10 minutes. Seeds can be dried in an oven for 2 to 3 hours at 55 to 60°C. Seeds obtained in the same season can germinate after slight scarification. Dry storage (6–14 months) increases the rates of seed germination of several types of cactus pear (Mondragon and Pimienta 1995). Seed viability is reduced after long-term storage. For instance, storage of seed lots for 9 years reduces the seed germinability by 50% (Muratalla et al. 1990). Temperature is the most important variable for cactus seed germination. For nineteen species of cacti the optimal temperature for seed germination ranges from 17 to 34°C with a mean of 25°C (Nobel 1988). Differences in germination have also been attributed to cultivar and seed condition. Seeds may have a physical dormancy due to the hard seed coat, which hinders germination. Several treatments have been reported to overcome this barrier. Scarifying seeds in hot water (80–90°C) twice and allowing them to cool to room temperature and then soaking them in distilled water for 24 hours promotes germination under greenhouse conditions in 10 to 17 days (Mondragon 1999). Seeds soaked in gibberellic acid (35 mg/liter) can germinate faster (Wang et al. 1996). Planting media should be kept moist for optimal germination of cactus pear seeds under greenhouse conditions.

Seedlings can be kept in germination trays until the first cladode grows to 10 to 15 cm. At this size, they can be transplanted to small pots (10 cm in diameter) or black plastic bags. Prior to transplanting, the entire tap root can be excised and the seedling allowed to dry for 5 to 7 days to promote healing and drying of the wounded tissue. Elimination of the tap root eases the task of transplanting and promotes formation of lateral roots, increasing the root volume and improving anchorage. Minimizing the time from crossed seed to a mature plant, ready for evaluation, is important for any breeding program. Cacti generally grow slowly, especially the columnar and spherical forms, under natural conditions. Most cacti respond to optimal conditions of water and nutrients (Nobel 1988). Other factors influencing this response include photoperiod (Sanderson et al. 1986) and atmospheric CO_2 concentration. Six-month-old *Opuntia* seedlings grown in a greenhouse can be transplanted to the field. At this age they may bear two or three slender pads and can be managed as adult plants or used as a source of vegetative material for grafting.

Plants of cactus pear derived from seeds tend to grow in an upright slender manner, branching only in the upper cladodes. By comparison, plants grown from cuttings tend to have thicker and wider cladodes as well as more pads on the lower part of the plants. Branching can be promoted in seedlings by pinching at the one-cladode stage. This practice encourages thickening of the basal cladode as well as branching, thus increasing photosynthetic area and improving anchorage and vigor. Pinching also allows for an early expression of adult cladode shape. Grafting is a potential method of reducing juvenility. By grafting immature cladodes onto mature cladodes, the scion (the detached plant part used in a graft) may have at least one flowering cladode in the next growing season, in comparison with the 4 to 6 years needed for seedlings transplanted to the field directly from the greenhouse.

Grafting is a standard practice to maintain rare forms of cacti, such as those lacking chlorophyll, cristate forms (Haage 1963; Pilbeam 1987; Pimienta and Muñoz 1995), and endangered species. Most information available pertains to spherical forms being used as scions and sharp angled forms of *Cereus, Hylocereus* spp., *Myrtillocactus geometrizans, Pereskia, Rhipsalis,* and *Trichocereus* being used as stocks (Pizzeti 1985). Grafting platyopuntias is a little more complicated. The main concern for *Opuntia* species is the shape and thickness of the stocks and scions. The best species to use as rootstocks is *O. ficus-indica,* because the plants are fast growing and almost spineless. Cultivars such as 'Seleccion Pabellon' available in Mexico for vegetable and forage production and 'Gialla' of Italy are also well suited for this purpose. Grafting can be performed

with young, full-size cladodes. The scion and stock should be selected and cut to match for size, shape, and thickness. To create matching shapes, both the donor cladode and the rootstock can be cut with the same device (e.g., an aluminum can with one edge sharpened to cut and act as a template at the same time). The scion should be placed carefully, trying to match the cambial tissues as closely as possible and maintained in place using rubber bands.

Clonal Propagation/Apomixis

New and superior cultivars need to be propagated as rapidly as possible for further trials and commercial production. Asexual propagation can be performed for cactus pear using stems (or portions thereof) of any age as well as flowers and unripe fruits. Commercial orchards typically rely on large pad fractions, whole pads, or short branches. A few specialized propagation nurseries have been attempted in Mexico with limited success, as cuttings are most often obtained from productive orchards using pruning residues. Efficient protocols for *in vitro* propagation are also available (Escobar et al. 1986; Villalobos 1995), but they are not used on a commercial scale due to the ease and lower cost of propagation from cladodes.

Apomixis, the formation of asexually derived embryos, is common in the genus *Opuntia* (Mondragon and Pimienta 1995). Polyembryonic seed percentages range from 0 to 50% for several *Opuntia* species and from 2 to 16% for several wild and cultivated cactus pear accessions. From a breeding perspective, polyembryony can be a problem during germination of crosses, because seedlings derived from somatic tissue will be identical to the female parent as opposed to a combination of the two parents. In general, identification of apomictic seedlings is relatively easy in the early stages of germination and seedling growth; however, some apomictic seedlings are indistinguishable from the zygotic seedling, and they tend to appear more similar as they become older. The apomictic seedling usually emerges later, is smaller, and is weaker than the zygotic seedling. Seedlings from polyembryonic seeds must be separated early in the germination phase of a program and some somatic seedlings will probably enter the evaluation phases of a breeding program (Mondragon and Bordelon 1996; Bunch 1997).

Future Directions

Cactus genetic research is in its infancy, and the vast majority of breeding work lies ahead. Several people who were fortunate enough to have worked with Dr. Barrientos have retold a story of his: you can cross two cactus pear varieties and obtain five species in the progeny. This story attests to the tremendous variability available among cactus pear and to the amount of work needed to sort out and harness this variability. With the increasing number of new and well-documented crosses performed in cactus programs around the world, the genetics behind many traits should be gradually revealed. Information from these crosses will help sort out taxonomic relationships and lend insight into the genetic control of some of the special characteristics and physiological systems that make cacti such remarkable plants (Nobel 1994).

As breeding efforts are continued, new and exciting research will unfold. Future projects may involve creating ploidy series of cacti of a specific genetic makeup. Also, in keeping with the sustainable nature of cacti and their potential to benefit regions of the world with limited resources, nutrient utilization of new cultivars must be investigated. Cultivars should be developed with enhanced ability to benefit from associations between rhizosphere organisms to increase productivity and reduce dependence on fertilizers. New biotechnological tools will help breeders meet their objectives as well as allow access to new sources of genetic variation. The ultimate goal will be to develop cacti into crops rivaling the best of other fruit, vegetable, and forage crops.

Biotechnology

An important complement to cactus breeding programs is the development of molecular tools to work with cacti. As has been demonstrated for numerous crop species, molecular biological tools can speed up the breeding process (Paterson et al. 1991; Staub et al. 1996), elucidate genetic mechanisms that cannot be easily dissected through plant breeding techniques (Paterson 1995), and in many cases can accomplish goals that are not possible through breeding. This section reviews the molecular work done on cacti and proposes a plan for the development of molecular tools for cacti utilizing the work done on traditional crop species.

Overview of Plant Molecular Tools

Most plant molecular genetics has focused on economically important crop species, such as corn or rice, or on facile models, such as *Arabidopsis.* The work done on other species can serve as a springboard to speed development of such tools for cacti. In turn, genetic analysis of cacti would pave the way for developing molecular programs for alternative crop species. A well-developed genetic map is important in this regard (Paterson et al. 1991; Staub et al. 1996). Genetic maps are constructed by utilizing highly variable, polymorphic molecular markers to assess levels of recombination in a cross between two variable parents. The

molecular markers serve as landmarks along the chromosomes of the organism and reflect underlying differences in the genomes of the two plants involved in the cross. Both hybridization-based markers, such as Restriction Fragment Length Polymorphisms (RFLPs), and PCR-based markers, such as RAPDs and Microsatellites, are routinely used. The ability of molecular markers to detect subtle changes in genome structure make them highly advantageous over traditional morphological markers for developing genetic maps of cacti. If a breeder attempts to move a cold-resistant phenotype from a wild *Opuntia* accession into a specific cultivar and lacks a molecular marker associated with cold resistance, all plants need to be grown to maturity and then tested for cold resistance. By contrast, if cold resistance is associated with a molecular marker, this marker can be screened in young plants, thus helping the breeder to make selections earlier in development.

Another important tool for molecular work is the ability to transform cactus plants with DNA fragments of interest. Although progress has already been made in this area (Zárate et al. 1998, 1999a), many hurdles remain. An important step is to generate stably transformed plants that can transmit the transgene of interest to subsequent generations through sexual crosses. For instance, if a gene conferring cold tolerance is isolated, it can be integrated into cultivated plant germplasm by transformation without having to worry about traditional breeding difficulties, such as making wide crosses or removing unwanted wild germplasm introduced into a cultivar when it is crossed with the wild plant. This is especially important for cacti, as the time from seedling to mature plant can be long, making the production of backcross populations time consuming. In addition, transformation allows genes to be transferred from plants that cannot be crossed with cacti, or even from other organisms. For instance, if one or a few genes controlling seediness can be identified, these genes could be inactivated through transformation of anti-sense constructs and screening for transformed plants that silence the seediness-related genes.

DNA and Protein Analysis

Molecular work done on cacti reveals a number of intriguing features. The polyploidy level varies, with a basal chromosome number of 11 (Pinkava et al. 1985, 1992). Analysis of nuclei from *Opuntia* TAM 1308 by flow cytometry indicates that they possess a DNA content similar to that of small genome crops such as sorghum and tomato. Isozyme analysis detecting variability among plants based on activity of known enzymes indicates a high level of variability among cacti, especially in pollen (Chessa et al. 1997). Other isozyme studies show a low variability among accessions but a curiously high variability among fruits and cladodes of the same cultivar (Uzun 1997). In contrast to isozyme studies, RAPD assays the variability of unknown DNA sequence fragments amplified using the Polymerase Chain Reaction (PCR). RAPD markers were used to verify the somatic origin of putative apomictic seedlings using seeds from two crosses of Mexican accessions (Mondragon 1999). The study indicated that seedling size and fresh weight are the only morphological features associated with the apomictic seedlings.

RAPDs have also been employed to compare DNA variability for relationships among *Opuntia* species with traditionally derived morphological classifications (Wang et al. 1998). Discrepancies occur between molecular and traditional classifications, although more work needs to be done to characterize these differences. A DNA extraction technique for cacti, which helps overcome the difficulties caused by mucilage, has been used for 32 accessions (Mondragon 1999).

Tissue Culture and Transformation

An efficient micropropagation protocol for cactus pear has been developed (Escobar et al. 1986). In particular, *in vitro* culture can produce virus-free plants and is a method for rapid propagation of new cultivars. The technique has not been used on a commercial scale due to the comparative ease of propagation through traditional methods. The production of somatic embryos (asexually formed embryos that arise from sporophytic cells unconnected with maternal tissues) occurs for a number of cactus species in tissue culture (Torres-Muñoz and Rodríguez-Garay 1996; Santacruz-Ruvalcaba et al. 1998). Ongoing work at the Federal University of Ceará in Brazil has led to a number of advances in both tissue culture and transformation techniques, such as callus and cell suspension cultures of *Opuntia* (Zárate et al. 1999c), cultivation of isolated shoot meristems, and regeneration of whole plants from the apical meristem (Zárate et al. 1999b). These tissue culture techniques have produced transient transformation of a β-glucuronidase reporter gene in callus and cell suspension cultures (Zárate et al. 1998) and in apical meristems (Zárate et al. 1999a). Analysis of seed reserve proteins in *Opuntia ficus-indica* (Uchoa et al. 1998) will be useful to research on improving cactus cultivars through transformation techniques.

Evolutionary Relationships

Much information from other plant species can be used for developing molecular tools for cacti. Understanding these

relationships will be key to using comparative mapping techniques to speed the development of a molecular map for cacti. Molecular sequence data for the plastid gene encoding the large subunit of Rubisco (rbcL) were obtained for a number of plant species, including some in the Cactaceae, from Genbank (http://www.ncbi.nlm.nih.gov/). The sequences were aligned using the Clustal alignment program (http://www-igbmc.ustrasbg.fr/BioInfo/ClustalX/Top.html), and phylogenetic trees were calculated via the parsimony method using DNAPars (available as part of the Phylip molecular phylogeny package; http://evolution.genetics.washington.edu/phylip.html). A consensus tree created using the majority-rule method (CONSENE, also in the Phylip package) indicates that the Cactaceae are most closely associated with the Aizoaceae. A well-characterized member of this family is *Mesembryanthemum crystallinum,* which also utilizes the CAM photosynthetic pathway. Closely associated to the Cactaceae are the Poaceae (grasses) and the Solanaceae. This tree is biased by the use of a gene involved in the photosynthetic machinery, which likely varies between CAM, C_3, and C_4 species. No phylogeny based on variation in a single gene can characterize the relationships between such a broad class of plant families. Hopefully, future molecular phylogenetic work will refine the position of the Cactaceae among other plant families.

Molecular Tools for Cacti

A first step in building molecular tools is to identify cactus sequences that relate to potentially useful genes in other taxa. This can be accomplished by hybridizing cactus clones with probes from other taxa and looking for expressed genes that are highly similar. To achieve this goal, a cDNA library will be constructed from *Opuntia* accessions from Texas A&M University-Kingsville. Genes recognized in other organisms involved in critical processes for cacti will be utilized. For example, cold-temperature-tolerance genes have been identified in *Arabidopsis* (Thomashow 1998) that might allow recognition of cactus genes involved in the same process. Other possibly useful genes to identify include those involved in drought/salt tolerance (Winicov 1998) and those uniquely involved in CAM (Cushman and Bohnert 1997).

The second step in developing cactus molecular tools will be to create a genetic map with the useful sequences providing the DNA markers. A mapping population of approximately 120 plants has been created by a cross between *Opuntia* accession TAM 1281 and *Opuntia* accession TAM 1250. Copies of this population are available in California, Georgia, and Argentina, and these plants will be used to create a genetic map of cacti with an average spacing of 5 cM between markers. The sequences identified will be used as RFLP probes to develop this map. Because of the morphological variability between the parents, and based on initial RAPD data, genetic polymorphism between the parents may be frequently encountered. This map will be publicly available, as will the clones from the mapping population, allowing other researchers to use and extend the map. Once an initial genetic map of cacti is created, morphological markers will be placed on the map. This will provide breeders a working framework and will also help characterize the interesting phenotypes associated with cacti.

Future Directions

Speeding the development of molecular tools for cacti using other well-studied plant genomes will provide workers interested in the molecular biology of cacti with a set of tools to accomplish their research goals. In addition, the localization of agronomic traits on the genetic map will allow breeders to use molecular techniques in their programs. However, the work described here is only an initial step toward the development and characterization of cacti at the molecular level. Another important goal should be the development of transformation systems for cacti. Because cacti may also be amenable to transformation using *Agrobacterium,* development of these systems could supplement and extend the work being done with particle bombardment. Research on tissue culture of cacti must be extended to provide a rapid system for the regeneration of transformed tissue into whole plants. Further work characterizing cactus germplasm using molecular markers can help create a better understanding of the relationships between available accessions. Cultivars have been recognized primarily by their morphological characteristics, which can be misleading (Wang et al. 1998). Molecular markers should be developed and utilized to evaluate germplasm resources, helping breeders determine the level of molecular similarity between two cultivars in a cross.

Another area of potential research is the study of chromosomal changes underlying the variable polyploid nature of the cactus genome. This has practical interest, because chromosomal imbalance associated with polyploidy may lead to partial seed set in *O. ficus-indica* (Nerd and Mizrahi 1994). Characterizing how polyploidy affects seed set may lead to the development of techniques to produce varieties with fewer seeds. In addition, physical maps of the cactus genome should be developed to allow researchers to identify and sequence genes of interest in cacti more easily. These tools should provide insight into the molecular basis

for many of the interesting phenotypes of cacti. The molecular characterization of these phenotypes will not only be intriguing within the framework of understanding cactus and plant morphology, but may also be potentially useful for the improvement of other crop species.

Conclusions

The Cactaceae exhibit many unique phenotypes, making it an ideal family for study by plant breeders and molecular biologists. This chapter has focused on the improvement of cactus germplasm via plant breeding and molecular techniques. Many modern varieties of cactus pear are the products of long-term, informal, yet effective selection by growers from plants in family gardens. These cultivars were selected in Mexico or were obtained from Mexican germplasm and adapted to other countries. More formal cactus pear breeding was attempted in the early 20th century in California and again during the 1970s in Mexico. Only recently have many of the advances and more formal techniques been utilized by research groups around the world. The molecular work done on cacti can benefit from biotechnological work on other species. Increased work in both breeding and biotechnology of cacti should provide significant insights into the processes that contribute to their unique phenotypes. Using these tools and techniques to accomplish the major objectives outlined in this chapter will improve cactus cultivars available to both farmers and consumers. Ultimately, breeding and biotechnology will play an important role in increasing the understanding and usefulness of cacti.

Acknowledgments

B.C. thanks Peter Felker for useful discussions and the Howard Hughes Medical Institute for a fellowship. Research of A.H.P has been funded by the International Arid Lands Consortium and the USDA Foreign Agriculture Service.

Literature Cited

Aguilar, B. A. 1987. Efecto de la aplicacion de acido giberelico (GA3) y urea en el fruto del nopal (*Opuntia amychlaea* Tenore). Master's Thesis, Colegio de Postgraduados, Chapingo, Mexico.

Barbera, G. 1995. History, Economic and Agro-ecological Importance. In *Agroecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 1–11.

Barbera, G., F. Carimi, and P. Inglese. 1991. The reflowering of prickly pear (*Opuntia ficus-indica* (L.) Miller): Influence on removal time and cladode load on yield and fruit ripening. *Journal of the American Society for Horticultural Science* 5: 77–80.

Barbera, G., F. Carimi, and P. Inglese. 1992. Past and present pole of the Indian-fig prickly pear (*Opuntia ficus-indica* (L.) Miller, Cactaceae) in the agriculture of Sicily. *Economic Botany* 46: 10–20.

Barbera, G., P. Inglese, and T. La Mantia. 1994. Influence of seed content on some characteristics of the fruit of cactus pear (*Opuntia ficus-indica* Mill.). *Scientia Horticulturae* 58: 161–165.

Bunch, R. 1997. Update on cactus pear breeding and new products at D'Arrigo Bros. *Journal of the Professional Association for Cactus Development* 2: 60–70.

Cantwell, M. 1991. Quality and postharvest physiology of "nopalitos" and "tunas." In *Proceedings of the Second Annual Texas Prickly Pear Conference.* McAllen, Texas. Pp. 50–66.

Chessa, I., G. Nieddu, P. Serra, P. Inglese, and T. L. Mantia. 1997. Isozyme characterizaton of *Opuntia* species and varieties from Italian germplasm. *Acta Horticulturae* 438: 45–52.

Corrales-Garcia, J., J. Andrade-Rodriguez, and E. Bernabe-Cruz. 1997. Response of six cultivars of tuna fruits to cold storage. *Journal of the Professional Association for Cactus Development* 2: 160–168.

Cui, M., P. M. Miller, and P. S. Nobel. 1993. CO_2 exchange and growth of the Crassulacean acid metabolism plant *Opuntia ficus-indica* under elevated CO_2 in open-top chambers. *Plant Physiology* 103: 519–524.

Cushman, J. C., and H. J. Bohnert. 1997. Molecular genetics of Crassulacean acid metabolism. *Plant Physiology* 113: 667–676.

Dreyer, P. 1985. *A Gardener Touched with Genius: The Life of Luther Burbank.* University of California Press, Berkeley.

Escobar, H. A., V. M. Villalobos, and A. Villegas. 1986. Opuntia micropropagation by axillary proliferation. *Plant Cell, Tissue and Organ Culture* 7: 269–277.

Felker, P. 1995a. Forage and fodder production and utilization. In *Agroecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 144–154.

Felker, P. 1995b. A review of cactus pear development in the United States. In *Memorias del VI Congreso Nacional y*

IV Internacional sobre el Conocimiento y Aprovechamiento del Nopal. Guadalajara, Mexico. Pp. 217–221.

Flores, V. C. 1995. "Nopalitos" production and processing. In *Agroecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 92–99.

Gil, G. S., and A. Espinosa. 1980. Desarrollo de frutos de tuna (*Opuntia ficus-indica* Mill.) con aplicación prefloral de giberellina y auxina. *Ciencia e Investigación Agraria* 7: 141–147.

Granata, G., and A. Sidoti. 1997. Appearance of *Alternaria* Golden Spot on cactus pear in Italy. *Acta Horticulturae* 438: 129–130.

Grant, V., A. K. Grant, and D. P. Hurd. 1979. Pollination of *Opuntia lindheimeri* and related species. *Plant Systematics and Evolution* 132: 313–320.

Haage, W. 1963. *Cacti and Succulents: A Practical Handbook.* Simon & Schuster, New York.

Hillig, K. W., and F. A. Iezzoni. 1988. Multivariate analysis of a sour cherry germplasm collection. *Journal of the American Society for Horticultural Science* 113: 928–934.

Hoffman, W. 1995. Ethnobotany. In *Agroecology, Cultivation and Uses of Cactus Pear.* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 12–19.

Loik, M. E., and P. S. Nobel. 1991. Water relations and muccoploysaccharide increases for a winter hardy cactus during acclimation to subzero temperatures. *Oecologia* 88: 340–346.

Loik, M. E., and P. S. Nobel. 1993. Freezing tolerance and water relations of *Opuntia fragilis* from Canada and United States. *Ecology* 74: 1722–1732.

Mondragon, J. C. 1999. Preliminary genetic studies on cactus pear (*Opuntia* spp. Cactaceae) germplasm from Central Mexico. Ph.D. Thesis, Purdue University, West Lafayette, Indiana.

Mondragon, J. C., and B. B. Bordelon. 1996. Cactus pear (*Opuntia* spp. Cactaceae) breeding for fruit production. *Journal of the Professional Association for Cactus Development* 1: 19–35.

Mondragon, J. C., and G. S. Perez. 1993. 'Reyna' (Syn. Alfajayucan) is the leading cactus pear cultivar in central Mexico. *Fruit Varieties Journal* 48: 134–136.

Mondragon, J. C., and S. G. Perez. 1996. Native cultivars of cactus pear in Mexico. In *Progress in New Crops* (J. Janick and J. E. Simon, eds.). ASHS Press, Alexandria, Virgina. Pp. 446–450.

Mondragon, J. C., and E. Pimienta. 1995. Propagation. In *Agroecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 64–70.

Muratalla, L. A., P. F. Barrientos, and A. J. Rodriguez. 1990. Germinación de semilla de nopal (*Opuntia amychlaea* T. cv. 'V5' y *O. ficus-indica* cvs. 'V1' y 'F1'). In *Memorias de la IV Reunion Nacional sobre el Conocimiento y Aprovechamiento del Nopal*. Zacatecas, Mexico. P. 19.

Nerd, A., and Y. Mizrahi. 1994. Toward seedless prickly pear. In *Proceedings of the Fifth Annual Texas Prickly Pear Council* (P. Felker and J. R. Moss, eds.), Kingsville, Texas. Pp. 5–6.

Nerd, A., and Y. Mizrahi. 1995. Effect of low winter temperatures on bud break in *Opuntia ficus-indica. Advances in Horticultural Science* 9: 1–4.

Nerd, A., and Y. Mizrahi. 1997. Reproductive biology of cactus fruit crops. *Horticultural Reviews* 18: 321–346.

Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti.* Cambridge University Press, New York.

Nobel, P. S. 1991a. Environmental productivity indices and productivity for *Opuntia ficus-indica* under current and elevated atmospheric CO_2 levels. *Plant, Cell and Environment* 14: 637–646.

Nobel, P. S. 1991b. Tansley Reveiw No. 32. Achievable productivities of certain CAM plants: basis for high values compared with C_3 and C_4 plants. *New Phytologist* 119: 183–205.

Nobel, P. S. 1994. *Remarkable Agaves and Cacti.* Oxford University Press, New York.

Nobel, P. S., and M. Castañeda. 1998. Seasonal, light and temperature influences on organ initiation for unrooted cladodes of the prickly pear cactus *Opuntia ficus-indica. Journal of the American Society for Horticultural Science* 123: 47–51.

Nobel, P. S., and A. A. Israel. 1994. Cladode development, environmental responses of CO_2 uptake, and productivity for *Opuntia ficus-indica* under elevated CO_2. *Journal of Experimental Botany* 45: 295–303.

Ortiz, H. Y. 1988. Efecto del acido giberelico y auxinas en el fruto del nopal tunero (*Opuntia amychlae* T.). Master's Thesis, Colegio de Postgraduados, Chapingo, Mexico.

Parish, J., and P. Felker. 1995. Evaluation of fruit quality and production of cold-hardy *Opuntia* fruit clones. In *Professional Association for Cactus Development First Annual Conference* (P. Felker and J. Moss, eds.), Kingsville, Texas. Pp. 12a–e.

Paterson, A. H. 1995. Molecular dissection of quantitative traits: progress and prospects. *Genome Research* 5: 321–333.

Paterson, A. H., T.-H. Lan, K. P. Reischmann, C. Chang, Y.-R. Lin, S.-C. Liu, M. D. Burow, S. P. Kowalski, C. S. Katsar, T. A. DelMonte, K. A. Feldmann, K. F. Schertz, and J. F. Wendel. 1996. Toward a unified genetic map of higher plants, transcending the monocot-dicot divergence. *Nature Genetics* 14: 380–382.

Paterson, A. H., S. D. Tanksley, and M. E. Sorrells. 1991. DNA markers in plant improvement. *Advances in Agronomy* 46: 39–90.

Pilbeam, J. 1987. *Cacti for the Connoisseur: A Guide to Growers and Collectors.* Timber Press, Portland, Oregon.

Pimienta-Barrios, E. 1990. *El Nopal Tunero.* Universidad de Guadalajara, Mexico.

Pimienta-Barrios, E.., and L. Mauricio. 1987. Variación en los componentes del fruto maduro entre formas de nopal (*Opuntia* spp.) tunero. *Revista de Fitotecnia Mexicana* 12: 183–196.

Pimienta-Barrios, E., and U. A. Muñoz. 1995. Domesticación of opuntias and cultivated varieties. In *Agroecology, Cultivation and Uses of Cactus Pear.* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 58–63.

Pinkava, D. J., M. A. Baker, B. D. Parfitt, M. W. Mohlenbrock, and R. D. Worthington. 1985. Chromosome numbers in some cacti of western North America—V, with nomenclatural changes. *Systematic Botany* 10: 471–483.

Pinkava, D. J., B. D. Parfitt, M. A. Baker, and R. D. Worthington. 1992. Chromosome numbers in some cacti of western North America—VI, with nomenclatural changes. *Madroño* 39: 98–113.

Pizzeti, M. 1985. *Guide to Cacti and Succulents.* Simon and Schuster, New York.

Saad, M., C. A. Degano, and J. Ochoa. 1998. Wet rot and necrosis caused by bacteria in *Opuntia ficus-indica* Mill. in Santiago del Estero, Argentina. *Journal of the Professional Association for Cactus Development* 3: 60–63.

Saenz, C., and E. Costell. 1990. Rheology of prickly pear (*Opuntia ficus-indica*) concentrated juices. In *Engineering and Food,* Vol. 1 (W. E. L. Spies and H. Schubert, eds.). Elsevier Applied Science, London. Pp. 133–137.

Sanderson, C. K., H. Yunn-Shy, C. W. Martin, and B. C. Reed. 1986. Effect of photoperiod and growth regulators on growth of three cacti. *HortScience* 21: 1381–1382.

Santacruz-Ruvalcaba, F., A. Gutiérrez-More, and B. Rodríguez-Garay. 1998. Somatic embryogenesis in some cactus and agave species. *Journal of the Professional Association for Cactus Development* 3: 15–26.

Silos-Espino, H., E. R. Salazar, Q. R. Cruz, J. O. Castro, and O. P. Lopez. 1999. Proteinas de reserva de importancia alimentaria del Nopal. In *Memorias del VIII Congreso Nacional y VI Internacional sobre el Conocimiento y Aprovechamiento del Nopal* (R. Aguirre and J. A. Reyes, eds.). San Luis Potosí, Mexico. Pp. 36–37.

Staub, J. E., F. C. Serquen, and M. Gupta. 1996. Genetic markers, map construction and their application in plant breeding. *Horticultural Science* 31: 729–740.

Sudzuki, H. F. 1995. Anatomy and Morphology. In *Agroecology, Cultivation and Uses of Cactus Pear.* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 28–35.

Thomashow, M. F. 1998. Role of cold-responsive genes in plant freezing tolerance. *Plant Physiology* 118: 1–7.

Torres-Muñoz, L., and B. Rodríguez-Garay. 1996. Somatic embryogenesis in the threatened cactus *Turbinicarpus pseudomarcrochele* (Buxbaum and Backeberg). *Journal of the Professional Association for Cactus Development* 1: 36–38.

Trujillo, A. S. 1986. Hibridización, aislamiento, y formas de reproducción de *Opuntia* spp. Master's Thesis, Colegio de Postgraduados, Chapingo, Mexico.

Uchoa, A. F., P. A. S. Souza, R. M. L. Zárate, E. Gomes-Filho, and F. A. P. Campos. 1998. The isolation and characterization of a reserve protein from the seeds of *Opuntia ficus-indica* (Cactaceae). *Brazilian Journal of Medical and Biological Research* 31: 757–761.

Uzun, I. 1997. Fruit and cladode isozymes in cactus pear. *Acta Horticulturae* 438: 53–56.

Villalobos, A. V. 1995. Tissue Culture application of *Opuntia* sp. micropropagation. In *Agroecology Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and

E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 71–77.

Wang, X., P. Felker, M. D. Burow, and A. H. Paterson. 1998. Comparison of RAPD marker patterns to morphological and physiological data in the classification of *Opuntia* accessions. *Journal of the Professional Association for Cactus Development* 3: 3–14.

Wang, X., P. Felker, and A. Paterson. 1997. Environmental influences on cactus pear fruit yield, quality and cold hardiness and development of hybrids with improved cold hardiness. *Journal of the Professional Association for Cactus Development* 2: 48–59.

Wang, X., P. Felker, A. Paterson, Y. Mizrahi, A. Nerd, and J. C. Mondragon. 1996. Cross-hybridization and seed germination in *Opuntia* species. *Journal of the Professional Association for Cactus Development* 1: 49–60.

Weiss, J., A. Nerd, and Y. Mizrahi. 1993. Vegetative parthenocarpy in the cactus pear *Opuntia ficus-indica* (L.) Mill. *Annals of Botany* 72: 521–526.

Weniger, D. 1984. *Cacti of Texas and Neighboring States: A Field Guide.* University of Texas, Austin.

Wessels, B. A. 1988. *Spineless Prickly Pear.* Perskor, Johannesburg.

Winicov, I. 1998. New molecular approaches to improving salt tolerance in crop plants. *Annals of Botany* 82: 703–710.

Zárate, R. M. L., F. A. P. Campos, and J. Landsmann. 1998. Establishment and transformation of callus and cell suspension cultures of the prickly-pear (*Opuntia ficus-indica*). *Journal of the Professional Association for Cactus Development* 3: 27–33.

Zárate, R. M. L., L. F. A. Ponte, J. Landsmann, and F. A. P. Campos. 1999a. Biolistic-mediated transient gene expression in shoot apical meristems of the prickly-pear (*Opuntia ficus-indica*). *Brazilian Archives of Biology and Technology* 42: 78–86.

Zárate, R. M. L., L. F. A. Ponte, J. Landsmann, and F. A. P. Campos. 1999b. Whole plant regneration from the shoot apical meristem of *Opuntia ficus-indica* (Cactaceae). *Journal of Applied Botany* 73: 83–85.

Zárate, R. M. L., C. Studart-Guimaráes, J. Landsmann, and F. A. P. Campos. 1999c. Establishment of callus and cell suspension cultures of *Opuntia ficus-indica* Mill. *Plant, Cell, Tissue and Organ Culture* 58: 155–157.

INDEX

Adhesives, 148–151

Adventitious roots, 8, 43–46, 169, 187

Agrobacterium tumefaciens, 245–246

Alcoholic beverages, 148–151, 158, 165

Algeria, 159, 200, 201, 202

Allozymes, 127–128

Alternaria golden spot, 245, 247–248

Ants, 79, 97, 99, 240, 241

Apical meristem: shoot, 30, 34, 35, 266; root, 42, 45–47, 49

Apomixis, 83–86, 265, 266.

Aposematic, 237, 239

Archaeology, 143, 146, 151, 159, 190, 222

Areoles, 3, 5, 34, 43, 75–76, 154, 262

Argentina, 1, 75, 168, 191, 201, 242–245, 262

Arid regions, 49, 75, 81–82, 109, 114, 126, 158, 167, 199–201, 204–205, 256, 258

Ariocarpus fissuratus, 24–25, 67

Armillaria, 245–246

Artificial selection, 144–145, 152, 154, 159

Atacama Desert, 70

Atmospheric CO_2, 63, 256

Australia, 84

Axillary buds, 34, 75

Aztec, 156, 222

Aztekium, 11, 44

Aztekium ritteri, 131

Backebergia militaris, 36

Bacteria and bacterial infections, 52, 177, 244–247

Bacterial spot, 245–247

Barrel cacti, 10, 11, 17, 62, 64, 68, 83, 91, 143, 148–151. *See also individual species*

Bats, 11, 77, 95, 102–103, 128, 154, 187

BCT clade, 9, 10, 12

Bees, 77–78, 95, 103, 191, 262

Betalains, 2, 222

Biodiversity, 91–92, 100, 103, 125–130, 136–138

Biological control, 235, 241, 243–244, 249, 250

Biomass productivity, 65–66, 170, 172, 201, 256

Biomechanics, 36, 69

Biotechnology, 255–257, 265–268

Birds, 93, 97–99, 102, 109, 110, 113, 116–119

Bison, 84

Bolivia, 201, 236, 244, 249

Boron, 52

Brazil, 191, 200, 201, 236, 243

Breeders and breeding, 127, 129, 256–265, 267–268

Breeding system evolution, 127–128

Brine (for nopalitos), 215–217
Burbank, Luther, 258, 260, 261
Burro, 119

C_3, 23, 26, 58, 60, 62, 63, 65, 68–69, 94
C_4, 26, 60, 62, 65, 68–69
Cacteae, 11
Cactoblastis cactorum, 84, 238–245, 250
Cactoideae, 5, 6, 8, 10, 16–17, 24, 26–27, 29–30, 33–34, 59
CactusNet, 179, 258
Cactus pear, 163–179, 236, 241, 244–251, 257–265. *See also* Cladodes; Fruits; *Opuntia ficus-indica*
Calcium (Ca), 202, 203, 207, 212
Calcium oxalate, 5, 7, 16, 17, 29, 42–43, 115, 202, 212
Calymmanthium, 8, 10
CAM. *See* Crassulacean acid metabolism (CAM)
Canada, 68, 84, 134, 165, 256, 257
Canary Islands, 157, 168, 228, 241
Candies, 218
Carbohydrate source/sink, 63
Carmine and carminic acid, 212, 222–224, 228, 240, 250
Carnegiea gigantea, 35, 36, 49, 58–59, 67, 69, 79, 94, 96, 98, 101
Caryophyllales, 2–3, 16
Casparian strip, 42
Cattle, 120, 147, 151, 200, 202–204, 206, 257
Cell cycle, 46
Cellulose, 202, 204–205, 207, 219. *See also* Cell walls
Cell walls, 26, 29, 30, 32, 37, 68
Cephalia, 32, 34–36
Cephalocereus columna-trajani, 25
Cephalocereus senilis, 29
Cerambycidae, 236–238, 250
Ceratitis capitata, 169, 237, 241–243
Cereus jamacaru, 186, 241
Cereus peruvianus, 186, 191–192, 194, 262
Cereus validus, 59, 62, 69
Chihuahuan Desert, 91, 95, 100–103, 145
Chile, 1, 75, 137, 165, 201, 203, 228, 242, 244, 245, 262
Chlorenchyma, 26, 52, 58, 62–63, 68
Chlorophyll, 26, 30, 36, 264
Chloroplast DNA (cpDNA), 2–3, 8, 11
Christmas cactus, 129
Chromosomes, 80, 86, 168, 186, 225, 227, 256, 259, 266, 267
CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), 131–136, 139
Clade, 2, 5, 10, 12, 14, 17
Cladodes: abiotic responses, 63; anatomy and morphology, 37; conservation and diffusion, 156–157; evolution and molecular aspects, 13, 264–265; human consumption, 169, 171, 212–213, 219–221; nonvertebrate consumption and interactions, 237, 242, 247–249; orientation, 58, 62, 179; vertebrate consumption, 109–115, 118, 120, 199–207, 203–207
CO_2 uptake, 58–66
Coccidae, 225
Cochineal, 147, 156, 157, 170, 212, 222–229. See also *Dactylopius*
Cold, resistance to, 83, 256, 258–260, 266, 267
Collared peccary, 112–115, 118, 120
Collecting and collectors, 129, 131, 133, 135–136, 139, 151, 155
Colombia, 186, 193, 201
Color-break, 173, 189, 191
Columnar cacti: abiotic responses, 66, 68; anatomy and morphology, 29, 34, 37; biotic responses, 77–78, 82, 91–92, 95–96, 98, 101, 103; conservation and diffusion, 125, 143–144, 146–155; evolution, 8, 10–13, 17; human consumption, 189–195, 264. *See also individual species*
Companion cells, 32
Consensus tree, 4, 9, 15
Conservation, 126, 129–139, 201–202
Convergent evolution, 7
Coreidae, 237, 241
Cortex, 26–27, 30, 37, 42–43
Cortical bundles, 30
Coryphantha, 2, 67, 93–94
Cosmetics, uses of cacti in, 221, 222, 223
Crassulacean acid metabolism (CAM), 1, 16, 23, 26, 58–59, 62, 70, 75, 194, 236, 239, 240, 256, 267
Crown gall, 245–246
Curculionidae, 236–237, 241, 250
Cuticle, 24, 37, 61, 69, 75, 178, 187, 236
Cylindropuntia, 14, 236, 238
Cylindropuntias, 42, 78, 84

Dactylopiidae, 236–238, 240, 241, 250
Dactylopius, 224, 226, 238, 240, 242
Dactylopius coccus, 222, 224–227, 229, 235, 238, 240, 250
Dactylopius opuntiae, 224, 238, 240–244
Deer, 112, 114, 120
Desert. *See specific deserts*
Desertification, 158–159, 200, 201

Diabetes mellitus, 219, 221, 229
Diarrhea, 115
Diaspis echinocacti, 236, 241–243, 250
Dichogamy, 79
Dietary fiber, for humans, 218–219
Digestibility, for animals, 203–207
Dioecy, 80, 128
Diptera, 237
Diseases, 236, 244–251, 256, 259
DNA, 2–3, 8, 11, 266, 267
Domestication, 143–155, 256, 257
Drought, 27, 29, 44, 48, 58, 61, 68, 81, 83, 200–201, 206, 256, 258, 259
Druses, 5, 7, 26, 29, 32

Easter cactus, 128–129
Echinocactus platyacanthus, 93
Echinocereus engelmannii, 93–94, 218
Echinocereus schmollii, 31
Echinocereus sciurus, 27–28
Echinopsis chamaecereus, 130
Ecuador, 186, 193
Eggstick, 239
Emasculation (flower), 262–264
Embolisms, 33, 51
Endangered species, 131–137, 151, 264
Endodermis, 42–43
Environmental Productivity Index (EPI), 64–66
Enzyme, 128–129. *See also* PEPCase; Rubisco
Epicuticular wax, 178
Epidermis, 25, 28, 29, 37, 43, 237, 246
Epiphyllum, 59
Epiphyllum phyllanthus, 43, 50–51
Epiphytes, 1, 3, 7, 8, 10, 17, 41, 43, 60–61, 70, 75, 78
Erosion (soil), 151, 158, 201–202
Erwina, 246
Escontria chiotilla, 28, 102
Espostoa melanostele, 36
Ethnobotany, 147–151
Evolution, 7, 14–17, 23, 75, 78, 80, 86, 97, 267; and animals/humans, 117, 119–120, 126, 128, 144, 236, 244

Fences, 148–151, 158
Ferocactus, 93
Ferocactus acanthodes, 27, 49, 51–53, 58–59, 63–65, 67, 69, 94, 218
Ferocactus peninsulae, 45–46, 48
Ferocactus wislizenii, 57, 67
Fiber, 202, 203, 207, 212, 218–219, 228
Firewood, 125, 148–151
Flower buds, 151
Flowers, 3, 7, 36, 76–82, 86, 95, 99; and animals/humans, 110–112, 116, 118, 125, 128–129, 147–151, 175–176, 249, 262–263
Fodder, 147–151, 199–202, 206–207, 260, 261
Foot rot, 245, 247–248
Forage, 160, 199–201, 204, 258, 265
Freezing damage, 58, 67, 83
Frost and frost tolerance, 83, 256, 258–260, 266, 267
Fruits, 3, 63–64, 82, 83, 97; development, manipulation, and production, 171–172, 174–177, 189, 191, 259; harvest, marketing, and selling arrangements, 166–167, 173–174, 179, 189, 195, 249, 256–257, 259–260; human consumption, 146–155, 158, 163–179, 185–195, 261, 265; nonhuman consumption, 109–112, 117, 242, 250; quality/sugars, 152, 173, 176–178, 189
Fundamental tissue, 26
Fungi and fungal infections, 176, 236, 244–250
Fungicides, 177, 179, 246, 247

Galápagos Islands, 79, 113, 115–120, 137
Genetic diversity, 126–128, 138
Geophytes, 3, 35, 44–45
Germination, 82–83, 92–94, 97, 99–100, 264
Germplasm, 128, 138–139, 168, 187, 255–256, 258–262, 266–268
Gibberellic acid (GA), 82, 92, 175, 177, 257, 264
Glochids, 113, 160, 165, 174, 176–179, 185, 257
Glucose, 219, 221
Goats, 204–206
Grafting, 264–265
Gray mold, 245, 249–250
Growth rings, 33–34, 37

Hailstorms, 167, 244, 246
Hallucinations, 125, 134
Harrisia, 12, 16, 235
Hatiora, 128–129
Hawkmoths, 7, 95, 103, 187
Heavy metals, 52

Hedges, 148–151, 158
Hemiepiphytes, 34, 60
Houses, 148–151, 218–219
Human diets, 143, 146–151, 218–219, 228
Hummingbirds, 7, 10, 11, 77, 95, 103
Hybridization, 69, 129, 257–259, 261, 265–267
Hydraulic conductivity (L_p), 50–51
Hylocereeae, 10, 17
Hylocereus, 8, 10, 12, 147
Hylocereus costaricensis, 186, 187, 193, 262
Hylocereus polyrhizus, 186–189, 193, 262
Hylocereus undatus, 59–61, 63, 75, 147, 155, 159, 185–189, 192–193, 194, 262
Hypodermis, 8, 16, 24–27, 29, 42–43

Idioblasts, 27, 29
Iguanas, 110, 112, 115, 118
Indian figs, 155, 157
Inferior ovary, 75
Insects, 93, 98, 117, 235–244, 256, 262
Intercellular air spaces, 26
IOS (International Organization for Succulent Plant Study), 6
Irrigation, 172–173, 176, 187, 191, 194, 260
Israel, 159, 168, 169, 174, 186–189, 191–193, 201, 258–260
Italy, 165–169, 174, 176, 201, 244, 245, 258, 259, 261, 264. *See also* Sicily

Jams, 147, 165, 217

L_p, 50–51
Larvae *(Cactoblastis),* 239, 240
Lateral roots, 43, 45–46, 48, 51, 264
Laticifers, 26, 29
Leaves, 3, 5, 13, 16, 24, 26, 29, 34
Lepidoptera, 242
Libriform fibers, 30, 32, 37
Life cycle, 97–100, 103, 225
Light, 58, 62, 99
Light responses, 58, 62, 64, 170. *See also* PPF Index (EPI)
Lignin and lignification, 36–37, 202, 219
Livestock. *See specific animals*
Lizards, 98, 110, 117
Lophocereus schottii, 94, 96
Lophophora, 3, 44–45
Lophophora williamsii, 134–135, 147
Low-temperature hardening, 66

Maihuenia, 5, 7, 27, 59
Maihuenioideae, 5, 6, 58
Mammals, 93, 98, 109, 111–112, 116, 119
Mammillaria, 11, 29, 77, 94
Mammillaria dioica, 52, 59, 67
Mammillaria magnimamma, 35
Markets and marketing: fruits, 166–167, 176, 178, 192–194, 256–257, 259–260; nopalitos, 215–217
Marmalades, 165, 212, 215, 217–218
Medicines, 147–151, 156, 219–221, 223
Mediterranean fruit fly, 169, 237, 241–243
Mediterranean region, 157–160, 163, 242–243, 249
Medullary bundles/rays, 27, 30
Melocactus peruvianus, 36
Mescaline, 7, 134
Mesoamerica, 143–147, 151, 156, 159, 221, 258
Metapopulation, 101
Metaxylem, 42
Mexico: cactus biotic responses, 75, 83–84, 91, 101, 103; conservation, diffusion, and evolution, 11, 133, 134, 137, 144–151, 156; human cactus consumption, 163, 165, 168, 169, 176, 178, 189, 190, 192, 193, 212, 214–217, 220–222, 256–262, 264, 265, 268; nonhuman cactus consumption and interactions, 114, 119, 200, 201, 224, 226–228, 242–245, 249
Microorganisms, 212, 214
Mites, 226, 237, 240
Mojave Desert, 137
Mold, 245, 249–250
Molecular biology, 6, 265–268
Moths, 7, 78, 95
Mucilage, 27, 50, 64, 151, 155, 214, 218, 219, 236, 239, 240, 263, 266
Mucilage cells, 8, 16, 25–29, 32, 42, 44
Mycorrhizae, 52
Myrtillocactus geometrizans, 93
Myrtillocactus schenckii, 25

Native American Church, 133–134
Nectar and nectary, 76–79, 95, 110–111, 116, 118, 128
Negev Desert, 168, 191
Neobuxbaumia macrocephala, 96
Neobuxbaumia mezcalaensis, 96, 159

Neobuxbaumia tetetzo, 93, 95–96, 98–100, 102, 159
Neoteny, 6
Net CO_2 uptake. *See* CO_2 uptake; Fruits; Photosynthesis
Nicaragua, 186, 193
Nitrogen (N), 52, 93, 172, 175, 202, 206, 207
Nocturnal acid accumulation, 62. *See also* CO_2 uptake; Crassulacean acid metabolism (CAM)
Nopal, 92, 113, 117
Nopalea, 29, 212, 257
Nopalea cochenillifera, 213, 224, 226
Nopaleras, 84, 85, 92, 101, 113, 120
Nopal flour, 219
Nopalito processing, 214–218
Nopalitos, 154, 157, 171, 212–218, 228, 257–258, 260, 261
Nopal products, 215–218
Notocacteae, 11
Nurse plants, 52–53, 92–95, 97, 99, 101
Nutrients, 51–52, 82, 99, 115, 117, 171–172
Nutrition (animal), 117, 202–207
Nymph (cochineal), 225

Obesity, 219, 221, 229
Opuntia, 12, 143–147, 155; anatomy and morphology, 26, 34; human consumption, 167, 220–221, 255, 260, 266; nonhuman consumption, 112, 203, 236, 239, 241–244, 246, 249–250; responses, 68, 83–86
Opuntia acanthocarpa, 59, 67, 218
Opuntia basilaris, 27, 59, 67, 218
Opuntia echios, 35, 138
Opuntia engelmannii, 203
Opuntia ficus-indica: abiotic responses, 59, 61–63, 66, 67, 69; anatomy and morphology, 37, 43, 45–46, 49, 51–53; biotic responses, 59, 61–63, 66, 67, 69, 75, 80–81, 85; conservation and diffusion, 128, 155–157; human consumption, 163–179, 212–215, 218, 256–257, 259–260, 263–264, 266–267; nonhuman consumption and interactions, 114, 199–207, 224, 236–241, 244, 247
Opuntia fragilis, 66, 67, 84, 85, 126
Opuntia humifusa, 59–60, 63, 66–68, 70, 126, 127
Opuntia leucotricha, 62
Opuntia littoralis, 69
Opuntia polyacantha, 59, 67, 202, 204
Opuntia rastrera, 85, 98
Opuntia robusta, 147, 203, 212, 214, 259
Opuntia streptacantha, 85, 98, 259
Opuntia stricta, 59, 84
Opuntia versicolor, 57
Opuntia violacea, 112
Opuntioideae, 5–7, 13–16, 24, 26–27, 33–34, 58–59, 236, 238
Orchard design and management *(O. ficus-indica),* 169, 174, 178
Ornamentals, 125, 128–129, 148–151, 156, 159
Osmotic pressure, 58, 63, 66, 68, 69
Outcrossing, 79–80, 86, 128
Overgrazing, 199, 205–206
Ovule, 77, 80, 82, 119
Oxalates, 5, 7, 16, 17, 29, 42–43, 115, 202, 212, 236

Pachycereeae, 10, 13, 16
Pachycereus pringlei, 31, 37, 45–46, 52, 59, 69, 76, 93, 96, 99–103, 128
Pachycereus schottii, 127
Packrats, 111–116, 120
Pads. *See* Cladodes
Parasitoids, 226, 239–240
Parthenocarpy, 257
Pathogens, 176–177
Peccary, 112–115, 118, 120
Penicillium, 250
Peniocereus striatus, 31
PEPCase, 58, 60, 63
Pereskia, 5, 7, 16, 27, 30, 59
Pereskia grandifolia, 35, 59
Pereskioideae, 5, 6, 26, 27, 33, 58–59, 236, 238
Pereskiopsis, 29, 59
Perianth, 77
Pericycle, 42–43, 48
Periderm, 26, 42, 51
Peru, 75, 201, 222, 223, 226, 228, 244, 249
Pests, 165, 169, 193, 222, 224–225, 229, 237–244, 250, 259
Petals, 110–112
Peyote, 134–135, 147
Phellem/Phelloderm, 48
Philippines, 186
Phloem, 30–32, 42, 63
Phoma sorghina, 245, 249–250
Phosphoenol pyruvate carboxylase (PEPCase), 58, 60, 63
Phosphorus (P), 52, 172, 202, 203, 206, 207, 212
Photoblastic, 92
Photoinhibition, 62

Photosynthetic enzymes. *See* PEPCase; Rubisco
Photosynthetic photon flux (PPF), 60–62, 93
Photosynthesis, 36, 57–58, 66. *See also* C_3; C_4; Crassulacean acid metabolism (CAM); CO_2 uptake
Phototropism, 58, 62
Phytochrome, 82
Phytophthora cactorum, 245, 247–249
Phytoplasmas, 244–245, 250
Pitahayas, 147, 185–186, 194–195
Pitayas, 147, 185–186, 194–195
Pith, 26–27, 29, 30, 32
Placentation, 3
Planting, of crops, 169, 174–175, 188, 194
Plant spacing *(O. ficus-indica),* 170–171, 174
Platyopuntia, 238
Platyopuntias, 12, 14, 155–160, 221, 264; anatomy and morphology, 27, 34, 37, 42; nonhuman consumption, 109–119, 199–207, 224, 227; responses, 58, 62–67, 69, 84
Pleistocene, 103, 112, 118, 120
Polaskia chende, 25
Pollen, 5, 77–81, 95, 110–111, 116–118, 128, 186, 262, 266
Pollination and pollinators, 7, 10, 77–82, 95–96, 99, 103, 118–119, 128, 187, 191, 257, 262–264
Polyploidy, 80, 85, 186, 256–257, 265, 267–268
Population and population dynamics, 98–100, 103
Postharvest: fruits *(O. ficus-indica),* 173, 176–178, 257; stems *(O. ficus-indica),* 213, 215
PPF Index (EPI), 64–65
Productivity (biomass), 65–66, 170, 172, 201, 256
Propagation, 134–135, 145, 159, 169
Protandry, 262
Protein, 117, 202–204, 207, 212, 266
Protozoa, 204–205
Pruning *(O. ficus-indica),* 170–171, 175–176
Pterocactus tuberosus, 35
Pubescence, 62
Pulp (fruit), 152, 176, 189, 193, 257
Pyralidae, 236–241, 250

Quiabentia, 59

Rabbits, 111–113, 115, 119
Radicle, 42–43, 46–47, 50
Rain, 60, 201, 240
Rain roots, 48
Random amplified polymorphic DNA (RAPD), 259, 266
Rathbunia alamosensis, 35
Rays, 32, 34, 37
Receptacle, 76–77
Reptiles, 98, 102, 110, 112, 116–117
Respiration, 52, 66, 212–213
Rhipsalideae, 10
Rhipsalis, 1, 30, 59, 129
Rhipsalis baccifera, 43, 51
Rhipsalis pentaptera, 129
Rhizosheaths, 50–53
Ribs, 5
Ribulosebisphosphate carboxylase/oxygenase (Rubisco), 58–60, 63
Ripening, of fruit, 173–174, 176, 189, 259
Rocks, 41, 49
Rodents, 98, 99, 102, 111, 113, 117, 118, 120
Root apical meristem, 42, 45–47, 49,
Root cap, 46
Root development and growth, 45–46, 169
Root hairs, 42, 46–47, 50
Root hydraulic conductivity, 50–51
Root respiration, 52
Roots and rooting system, 42–45, 69, 202
Root/shoot ratio, 49, 51, 52
Root-soil air gaps, 51
Root spurs, 46
Rot, 245–247
Rubisco, 58–60, 63, 267
Ruminants, 202–207

Salinity, 62–63, 69, 168, 172, 191
Sap suckers, 238, 240, 242
Schlumbergera, 128–129
Sclerids, 29, 31–32
Scozzolatura, 158, 164–166, 174–176
Seed coat and seed testa, 82
Seed dispersal and germination, 82–83, 92–94, 97, 99–100, 264
Seedlings, 50, 53, 83, 92–94, 99–100, 264, 266
Seeds, 42, 147–151, 153–154; evolutionary/molecular aspects, 2, 5, 7, 14, 257–258, 264, 266, 267; human consumption, 165, 176, 179, 186, 188; nonhuman consumption, 109–111; responses, 82–83, 85, 92–93, 99

Selenicereus, 8, 10
Selenicereus megalanthus, 186, 187, 189, 193, 262
Semiarid regions, 66, 75, 84, 117, 126, 168, 199–201, 204, 239, 256, 258
Sheep, 200–207, 257
Shelf life: fruits, 176, 178, 179, 189, 190, 192, 194; stems, 213–214
Sicily, 157–158, 164, 166–167, 170, 260, 261
Sieve tubes, 32
Silica bodies and grains, 28, 29
Sink, carbohydrate, 63, 171, 175
Sodium (Na), 62, 69, 202, 203, 206, 207, 212
Soft rot, 245–247
Soil, 51, 53, 69, 92–93, 99, 103, 249
Soil erosion, 151, 158
Soil water content, 169
Solar irradiation, 61
Sonoran Desert, 46, 49, 52, 65, 79, 92, 94, 97, 100–102, 145, 174, 218
Source/sink, 63, 171
South Africa, 164, 168, 169, 201, 239, 241, 243, 244, 249, 258–262
Spacing, plant *(O. ficus-indica),* 170–171, 174
Spines, 3, 10, 34–36, 62, 115, 118, 165, 226, 257, 258
Stamens, 76–79, 263
Starch, 27, 30, 42, 44, 64, 82, 189
Stele, 30, 32
Stem area index (SAI), 65–66, 170–171
Stenocereus, 12, 84, 102, 189, 193
Stenocereus griseus, 186
Stenocereus gummosus, 28, 45–48, 50, 52, 98
Stenocereus pruinosus, 152, 159
Stenocereus queretaroensis, 59–60, 62–63, 67, 75, 81–82, 151–152, 159, 185–186, 190–191, 194
Stenocereus stellatus, 151–154, 159, 186, 190–191
Stenocereus thurberi, 52, 67, 93, 95–97, 128
Stigma, 76–77, 79–80, 119, 263
Stomata, 24, 26, 58–61, 68, 75, 246
Style, 76–77, 80, 119, 263
Sugars, 173, 189, 202, 205–207, 219, 246
Surface area–volume ratio, 8
Survival, 66–69

Taiwan, 186, 187–188, 192
Tannins, 31–32
Taproots, 44–45, 49
Tehuacán Valley, 46, 91, 94, 96, 100–101, 103, 146–147, 151–154
Temperature, 60, 66–68. *See also* CO_2 uptake
Temperature Index (EPI), 64–65
Threatened species, 131–137, 139
Tissue culture, 266, 267
Tortoises, 110, 112, 115, 118, 119
Tracheids, 5, 6
Transpiration, 24, 60, 75
Tree, consensus, 4, 9, 15
Trichocereus, 67, 95
Trichomes, 7, 35–36
Trioecy, 80, 128
Tubercles, 29, 257
Tuberous roots, 44
Tunas, 155, 157
Tunisia, 159, 200–203

United States: conservation, 132, 134, 137; human cactus consumption, 165, 168, 169, 175, 186, 193, 256, 257, 259–261; nonhuman cactus consumption, 201, 203, 222, 224, 242

Vascular cambium, 32, 34
Vascular cylinder/tissue, 30, 42. *See also* Phloem; Xylem
Vascular (wide-band) tracheids, 30–34, 37
Vegetable (nopalitos), 154, 157, 171, 212–218, 228, 257–258, 260, 261
Vertebrates (wild), 109–120. *See also specific animals*
Vessels, 30, 32–33, 42–43
Vietnam, 186, 187, 192
Vine cacti, 185–189, 192–195
Viruses, 244–245, 250
Vitamins, 176, 207

WANA (West Asia/North Africa) region, 199–207
Water Index (EPI), 61, 64–65
Water relations, 61, 205, 236
Water storage capacity, 44, 81
Water stress, 27, 29, 44, 48, 58, 68, 113
Water-use efficiency, 60–61, 172, 201
Wax (cuticle), 178
Weberbauerocereus weberbaueri, 96, 127
West Asia/North Africa (WANA) region, 199–207

Wide-band tracheids, 30–34, 37
Wilcoxia poselgeri, 28, 31
Wild cochineal, 222, 226–227
Wind, 41, 69, 97, 158, 201, 202
Wood, 32–34, 36–37, 69
Wounds/wound pathogens, 177, 245–246, 263
Xoconoztles, 147, 154
Xylem, 30, 32, 42–43, 69
Yeasts, 244–247
Zoochory, 97

Designer:	Barbara Jellow
Compositor:	BookMatters, Berkeley
Text:	10¼/13 Adobe Garamond
Display:	Adobe Garamond
Printer and Binder:	Malloy Lithographing, Inc.